FINE-SCALE DISTURBANCE AND STAND DYNAMICS IN MATURE, SPRUCE-SUBALPINE FIR FORESTS OF CENTRAL BRITISH COLUMBIA

by

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ABSTRACT

Fine-scale disturbance and stand dynamics within mature, spruce-subalpine fir forests were compared and contrasted across the central interior of British Columbia. The central interior is ideal for the study of fine-scale disturbance because sub-boreal and subalpine ecosystems span the dry interior plateau and grade eastward into the progressively wetter, cooler, high-elevation ecosystems of the Rocky Mountain Foothills. Three biogeoclimatic variants where selected across this climatic gradient: the dry-warm Sub-Boreal Spruce (SBSdw3), the wet-cool Sub-Boreal Spruce (SBSwk1), and the wet-cool Engelmann Spruce-Subalpine Fir (ESSFwk2). Traditional and newly developed dendroecological techniques were used to identify the effects of past intermediate- and coarse-scale disturbance events, and to infer regional climate fluctuations, in order to separate these from the effects of fine-scale disturbance. Periods of canopy mortality occurred in the ESSFwk1 variant during the 1710s and 1830s, in the SBSwk1 variant during the 1830s and 1870s, and in the SBSdw3 variant during the 1870s. Based on historical documentation and dendroecological evidence, these periods of canopy mortality were likely caused by spruce beetle, and there is strong evidence of notable shifts in species composition. A western balsam bark beetle outbreak occurred in the ESSFwk2 variant during the 1920s and 1930s, and tree ring analyse provides strong evidence that species dominance shifted from subalpine fir to spruce within these stands. Moran's I analysis of canopy ascension dates suggests that fine-scale disturbance is random in space and time across all ecological variants. Canopy openings caused by disturbance averaged ≈2.5 m in diameter, which is equivalent to the average distances between nearest neighbours. Decadal disturbance rates did not differ by variant ($p = 0.117$) or by species nested within variant ($p = 0.418$). Although the decadal disturbance rates did not differ by variant, mean rates within SBSdw3, SBSwk1, ESSFwk2 variants were 7.4, 6.4

and 5.0 %, respectively. The results of this research indicate that fine-scale disturbances are important ecological processes in sub-boreal and subalpine forest ecosystems. Within these ecosystems, however, there is considerable overlap between disturbance types of varying spatial and temporal scales. Intermediate- and coarse-scale disturbance events, such as those caused by insects (e.g., spruce beetle and western balsam bark beetle), have been more influential in causing distinct changes in stand structure and composition than fine-scale disturbances. Consideration of disturbance events at multiple scales, however, shows that fine-scale disturbance does exhibit continuous stand level maintenance and renewal.

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PREFACE

"To have the ultimate, even if idealistic, objective of fusing the shattered fragments into the original unity is of great scientific and practical importance; practical because so many problems in nature are problems of the ecosystem rather than of soil, animals or plants, and scientific because it is our primary business to understand." *Alex. S. Watt, 1947.*

Forest management within British Columbia has traditionally been biased towards sustaining fibre yields. Arguably, this bias still remains as the dominant management framework today. Present forest health concerns, however, have forest managers re-evaluating how forested ecosystems should be managed. Although in its youth, a paradigm shift is occurring in British Columbia, and this is changing the way we approach forest management. The new approach, although in debate as to its appropriateness across a wide range of ecological and tenure systems, is based on two premises. First, successful conservation and maintenance of healthy forest ecosystems requires knowledge pertaining to historical patterns and processes resulting from naturally occurring disturbance events (e.g., the spatial and temporal distribution of forest patches caused by wildfire). Second, ecological values inherent in forest ecosystems are best maintained by using forest practices that mimic these natural disturbances. Together, these premises define forest ecosystem management (Attwill 1994, Rogers 1996, Bergeron *et al.* 1999).

This thesis adds to the knowledge base that is essential for examining the application of forest ecosystem management. The objective of this thesis was to quantify and characterize fine-scale disturbance patterns and processes as they vary across three distinct sub-boreal and subalpine ecosystems of central British Columbia. In British Columbia, the central interior is ideal for the study of fine-scale disturbance because sub-boreal and subalpine ecosystems span the dry interior plateau and grade eastward into the progressively wetter, cooler, high-elevation ecosystems of the Rocky Mountain Foothills (Meidinger and

Pojar 1991). My research goals were to: (1) develop and modify existing dendroecological techniques to date fine-scale disturbance; (2) quantify present forest composition and structure as it relates to unique disturbance events; and (3) determine the spatial and temporal occurrence of fine-scale disturbance within and between three climatically distinct, mature spruce-subalpine fir forest ecosystems.

In Chapter 1, I review the general forest ecology, current understanding of stand dynamics and disturbance ecology set in the Sub-Boreal Spruce and Engelmann Spruce – Subalpine Fir biogeoclimatic zones. Although coarse-scale disturbance events, such as stand-replacing fires, play a significant role in shaping these ecosystems, fine-scale disturbance events can have an impact on the forest structure and dynamics at the stand level.

In Chapter 2, I develop a set of stand and landscape-level standardized chronologies to identify past growing conditions attributed to disturbances and climatic events at scales greater than the sampling unit (50-m × 50-m plots). To characterize fine-scale disturbance regimes in any region, historical legacies created by past intermediate- and coarse-scale disturbance events and the regional climate influence must be documented. In the first standardization method, crossdated series were transformed by dividing the observed ring-width by the mean series ring-width (i.e., horizontal-line standardization). Standardizing series by their mean preserves long-term growth trends that can be used to identify intermediate- and coarse-scale canopy removal. In the second standardization method, crossdated series were transformed by fitting a cubic-smoothing-spline of 50 % frequency response of 50 years. Standardizing series using a cubic-spline preserves short-term growth trends that can be used to infer yearly climatic fluctuations. These two chronologies were used to aid in: (1) the reconstruction of individual stand histories; and (2) the explanation of

differences in stand structure, composition and forest dynamics across the three sub-boreal and subalpine ecosystems.

In Chapter 3, I develop methods to use radial-growth-rate patterns in present canopy trees to determine dates of ascension towards the canopy. Two growth-rate criteria were calibrated for the sub-boreal and subalpine ecosystems, including: (1) early growth rates that indicate gap-origin of sample trees; or (2) release criteria that indicate that a sample tree released from suppression due to overhead mortality. The release criteria were calibrated using a sample of gap-maker/gap-filler pairs with known dates of death and response. Despite a conservative release threshold, analyses revealed that a substantial number of release events, attributed to climate, were being counted.

In Chapter 4, in response to the problem identified with the release threshold defined in Chapter 3, I develop a new dendroecological method to separate responses to overhead tree mortality from climate. Divergence from the regional year-to-year signal was used to assess an individual tree's growing state at fine-scales ($\leq$0.25 ha). The year when an individual series diverges from the regional trend, to some degree for an extended length of time, was used to separate responses to overhead tree mortality from climate.

In Chapter 5, I summarize the fine-scale disturbance regimes of the three climatically distinct, mature spruce-subalpine fir ecosystems. This study combines the results and methodologies developed in Chapters 2, 3 and 4 to develop fine-scale disturbance chronologies for each plot. Basic stand composition and attribute data were sampled. Spatial autocorrelation analysis of final ascension dates and point-pattern analysis of living and dead trees were used to determine differences in the canopy level disturbance structures across the three climatically distinct ecosystems.

In Chapter 6, the results of the individual studies are integrated, drawing final conclusions regarding the fine-scale disturbance regimes within the mature, spruce-subalpine fir forests types studied within this thesis. Furthermore, in Chapter 6, I discuss the possible implications for forest management and suggest future research directions within the mature, spruce-subalpine fir forests found across central British Columbia.

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CHAPTER 1 - ECOLOGY, FOREST DYNAMICS AND DISTURBANCE AGENTS OF THE SUB-BOREAL SPRUCE AND ENGELMANN SPRUCE-SUBALPINE FIR BIOGEOCLIMATIC ZONES

Introduction

Within the central interior of British Columbia there is a climatic gradient that spans the dry interior, sub-boreal plateau to progressively wetter, cooler, high-elevation, subalpine ecosystems of the Rocky Mountain Foothills (Meidinger and Pojar 1991). Within these forested ecosystems fire has historically been thought of as the most important disturbance agent (Johnson 1992, Andison 1996, DeLong and Tanner 1996, Hawkes *et al.* 1997, DeLong and Kessler 2000). A review of the ecology, forest dynamics and disturbance literature within the sub-boreal and subalpine ecosystems suggests that fire may not always be the principal agent of disturbance controlling stand structure and composition (Hawkes *et al.* 1997, Parish *et al.* 1999, Antos and Parish 2002a, Antos and Parish 2002b). For example, Parish *et al.* (1999) found that stand composition of a mature spruce-subalpine fir forest in southeastern British Columbia, was the result of multiple disturbance types of differing intensities acting at multiple spatial scales. This overlapping of disturbance types supports White's (1979) hypothesis that a gradient between major and minor disturbance events, rather than a uniquely definable set of major catastrophes, can exist. The objectives of this chapter are to: (1) review the general ecology, stand dynamics and disturbance regimes within the sub-boreal and subalpine forest ecosystems; and (2) review the most common agents of disturbance influencing forest ecology in the central interior of British Columbia.

Classification of British Columbia's forested ecosystems

The terrestrial ecosystems of British Columbia have been hierarchically classified using the biogeoclimatic ecosystem classification system (Meidinger and Pojar 1991). This system integrates climate, soil, and vegetation data, and attempts to provide a universal framework for resource management and scientific research (Meidinger and Pojar 1991). The biogeoclimatic subzone is the basic unit of classification, resulting from zonal (climatic) categorization, and subzones represent groups of ecosystems under the influence of the same regional climate (DeLong *et al.* 1993). Subzones can be grouped to form biogeoclimatic zones and subdivided to define ecological variants. The variant reflects a further differentiation in regional climate and is generally recognized as an area that is slightly drier, wetter, snowier, warmer, or colder than other areas within the same subzone (Meidinger and Pojar 1991). Similar climax vegetation can occur over a range of subzones and variants, and in extreme cases among biogeoclimatic zones. As a consequence, similar climax-forest communities may represent ecosystems from different regional climates and with different soils (Meidinger and Pojar 1991).

The Sub-Boreal Spruce (SBS) and Engelmann Spruce-Subalpine Fir (ESSF) are two of the dominant biogeoclimatic zones of central and east-central British Columbia. In contrast to true boreal ecosystems, the sub-boreal and subalpine climates are slightly less continental, thus slightly warmer in January and cooler in July (Meidinger and Pojar 1991).

General description of the Sub-Boreal Spruce Zone

The SBS biogeoclimatic zone is located within central British Columbia. It is bordered by the Interior Cedar Hemlock (ICH), Sub-Boreal Pine-Spruce (SBPS), Interior Douglas-fir (IDF) and Engelmann Spruce-Subalpine Fir (ESSF) zones. It occurs from valley

bottoms up to 1100-1300 m elevation and between 52 and 57 °N latitude and 122 and 128 °W longitude (Meidinger and Pojar 1991).

Due to its moderate boreal climate, the SBS is affected by seasonal extremes in temperature and by relatively moderate levels of precipitation. The region is broadly continental with long, cold, snowy winters and short, warm, moist summers (DeLong *et al.* 1993). Mean annual temperature of the SBS ranges from 1.7-5 °C and average temperatures are below 0 °C for 4-5 months of the year, and above 10 °C for 2-5 months (Meidinger and Pojar 1991). Mean annual precipitation, recorded at long-term stations, ranges from 440-900 mm, of which 25-50 % is snow (Meidinger and Pojar 1991). Upland soils are primarily from the luvisolic, podzolic, and brunisolic soil orders found on abundant morainal deposits and imperfectly to poorly drained sites typically will display gleyed soil horizons (Meidinger and Pojar 1991, Agric. and Agri-Food Can. Publ. 1998).

The SBS zone is dominated by upland coniferous forest types. Hybrid white spruce (*Picea engelmannii* × *glauca* Voss x Parry) and subalpine fir (*Abies lasiocarpa* Nutt.) are the dominant climax tree species. Lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.), a seral species in the SBS zone, is common in mature forests in the drier parts of the zone and both lodgepole pine and trembling aspen (*Populus tremuloides* Michx.) pioneer the extensive seral stands (Meidinger and Pojar 1991). Paper birch (*Betula papyrifera* Marsh), another pioneer species, will establish on moist, rich sites. Douglas-fir (*Pseudotsuga menziesii* Franco), a long-lived species, will occur abundantly on dry, warm, rich sites as a consistent, although small, component of mesic forest types.

Ten subzones are recognized within the SBS zone, largely due to variability in climate, especially precipitation (Meidinger and Pojar 1991). Within this study, I will

consider two biogeoclimatic variants (Figure 1.1): the Stuart Dry Warm Sub-Boreal Spruce (SBSdw3) and the Willow Wet Cool Sub-Boreal Spruce (SBSwk1) (Meidinger and Pojar 1991). The former variant falls within DeLong's (2002) Moist Interior - Plateau Natural Disturbance Unit (NDU) with fire and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) as the key stand-replacement disturbance agents. The disturbance cycle assigned to this NDU is 100 years (DeLong 2002), supported by the work of Andison (1996) and DeLong (1998). The latter variant falls within the McGregor Plateau NDU with fire as the key stand-replacement disturbance agent (DeLong 2002). The stand-replacement-disturbance cycle assigned to this unit by DeLong (2002) is 220 years.

General description of the Engelmann Spruce-Subalpine Fir Zone

The ESSF biogeoclimatic zone is one of the most extensive forest zones in British Columbia, covering 13.3 million ha or 14 % of BC's land area (Jull *et al.* 1996). It is the uppermost forested area in elevation, the widest ranging biogeoclimatic zone in British Columbia, and found in Alberta, the Pacific Northwest and Rocky Mountain states. In British Columbia, the ESSF zone occurs at elevations of 1200-2100 m in the south-west, from 1500-2300 m in the south-east and from 900-1700 m in the northern part of the zone (Meidinger and Pojar 1991). In east-central British Columbia it is found on the McGregor Plateau below the Alpine Tundra (AT) zone and above the SBS and ICH zones. The McGregor Plateau is at the eastern edge of the interior plateau, between the northern and southern portions of the Rocky Mountain trench (DeLong *et al.* 1994).

At elevations >1000 m, the climate is cold and precipitation is variable with windward slopes being wetter than lee slopes (DeLong *et al.* 1994). The ESSF zone has a cold, moist, snowy continental climate. In the southern regions of British Columbia, mean

annual temperatures range from −2 to 2 °C (Meidinger and Pojar 1991). Mean monthly temperatures are below 0 °C for 5-7 months and above 10 °C for 0-2 months (Meidinger and Pojar 1991). Although precipitation is highly variable, windward slopes can receive up to 2200 mm annual precipitation. Most of the precipitation (50-70 %) falls as snow and maximum snow pack ranges from 1-4 m (Meidinger and Pojar 1991). Due to the short cool growing seasons, and long cold winters, the ESSF zone is one of the most severe climates for forest growth and regeneration (Jull *et al.* 1996).

Within east-central British Columbia, at the lower elevation range, soils are predominantly brunisols, luvisols and podzols (see Agric. and Agri-Food Can. Publ. 1998). Humo-ferric podzols have formed on parent materials consisting predominantly of medium textured morainal and colluvial deposits (DeLong *et al.* 1994).

The ESSF zone includes continuous forest at its lower and middle elevations, and subalpine parkland at its upper elevations (Meidinger and Pojar 1991). At lower elevations the ESSF zone is dominated by Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa*). Spruce, which is the longer-lived species, usually dominates the canopy of mature stands despite its relatively limited recruitment in the understory (Veblen 1986, Meidinger and Pojar 1991, Veblen *et al.* 1991, Veblen *et al.* 1994, Kneeshaw and Burton 1997, Lewis and Lindgren 1999, Lewis and Lindgren 2002).

Fifteen forested subzones are currently recognized in the ESSF zone (Meidinger and Pojar 1991), largely due to the broad latitudinal and elevation range, and to the variability in climate, especially precipitation. Within this study, I will consider one biogeoclimatic variant (Figure 1.1), the Misinchinka Wet Cool Engelmann Spruce-Subalpine Fir (ESSFwk2) (Meidinger and Pojar 1991). This variant falls within DeLong's (2002) Wet Mountain NDU

with stand-replacement disturbance events occurring at irregular intervals with as much as 1000 years between such events on any site.

Stand dynamics within the SBS and ESSF

There are recognizable and seemingly equivalent patterns and processes that appear after stand-replacing disturbances. Models of stand dynamics, therefore, are fundamental in understanding stand genesis, maintenance, and renewal over long periods of time. The progressive change in vegetation has lead to the development of two competing models of forest succession. The first, where one species invades after another, until one species or a group of species invades, predominates and replaces itself rather than being replaced, is known as relay floristics (Clements 1916, Oliver and Larson 1996). This process of replacement creates a stable endpoint to succession known as the "steady-state", "equilibrium" or "climax" vegetation association (Clements 1916, Oliver and Larson 1996). The second, where species that predominate later have been present since, or almost immediately after, the stand replacing disturbance event is known as initial floristics (Egler 1954, Drury and Nisbet 1973).

Due to the stochastic nature of most disturbance types, variability exists in the potential stand development for a given area. Elements of both initial and relay floristics, thus, are characteristic of stand development. The invasion patterns after disturbance, however, predominantly follow the initial floristics pattern (Oliver and Larson 1996). As a direct outcome of the latter model, Oliver and Larson (1996) proposed four distinct successional phases that characterize the progression of forest succession. These phases are (1) stand initiation, (2) stem exclusion, (3) stem reinitiation and (4) old-growth. This stand-dynamics model has been applied to SBS and ESSF biogeoclimatic zones, and comparable

forest types (Aplet *et al.* 1988, Kneeshaw and Burton 1997, Lewis and Lindgren 1999, Newbery 2001, Antos and Parish 2002a, Antos and Parish 2002b). Stand dynamics and disturbance ecology studies within the SBS and ESSF biogeoclimatic zones, however, suggest that the theoretical phases of the traditional models are not ecologically strict (Antos and Parish 2002a, Antos and Parish 2002b).

The relative importance of coarse-scale (e.g., wildfire) versus fine-scale processes on stand structure and dynamics are currently under review (Kimmins 1999, McCarthy 2001). Stands initiated by fire are subsequently affected by various partial disturbances (Agee 1993, Antos and Parish 2002a). Under certain circumstances, however, legacies from the initial stand-replacing events can continue to dominate stand structure and dynamics; even with long periods between stand-replacement (Antos and Parish 2002a). In contrast, some sub-boreal and subalpine forest types are strongly influenced by single and multiple-tree disturbance events (Veblen 1986, Lertzman and Krebs 1991, Lertzman 1992, Kneeshaw and Burton 1997, Lewis and Lindgren 2000, Newbery 2001). This range from coarse- to fine-scale disturbance types, coexisting on the landscape, supports White's (1979) hypotheses that: (1) there is a gradient from major to minor disturbance events rather than a uniquely definable set of major catastrophes; and (2) some disturbances are initiated or promoted by the biotic component of the ecosystem.

SBS and ESSF as fire driven ecosystems

The role of fire as a natural process vital to the health and renewal of boreal, sub-boreal and sub-alpine forests of western North America has long been acknowledged (Johnson and Rowe 1977, Hawkes 1980, Romme 1980, Heinselman 1981, Pyne 1984). More recently, the SBS and ESSF biogeoclimatic zones of central and east-central British

Columbia have received greater attention with respect to stand-replacing fires, which have historically been thought of as the most important natural disturbance agent (Johnson 1992, Andison 1996, DeLong and Tanner 1996, Oliver and Larson 1996, Hawkes *et al.* 1997, DeLong 1998). Although the SBS and ESSF forests, in most cases, do originate by fire, recent studies have shown that the time between stand-replacing events are enormously varied (Hawkes *et al.* 1997, Sanborn *et al.* 2001). In these forest types, fire may be so infrequent that the development of true old-growth forests may be possible. Hawkes *et al.* (1997) report that fire return intervals in very wet and cool SBS subzones near the Rocky Mountains likely range from 1200-6250 years. DeLong and Tanner (1996) reported return intervals ranging from 227-345 years in slightly drier SBS forests in the foothills of the Rocky Mountains.

As the role of fire diminishes, other biotic patch disturbance agents could assume a dominant role in renewal of boreal, sub-boreal and sub-alpine forests. A number of the biotic patch disturbance agents important within the SBS and ESSF are discussed below.

SBS and ESSF as patch driven ecosystems

At sporadic intervals a limited number of insect species have the ability to initiate patch disturbances (Lewis and Lindgren 2000). Among these insects are the primary bark beetles and a number of defoliating insects. The most common patch-initiating agent in mature, spruce-subalpine fir forests of central British Columbia is the spruce beetle (*Dendroctonus rufipennis* Kirby).

The spruce beetle can cause severe mortality at regular intervals (Humphreys and Safranyik 1993). Outbreaks often follow severe windthrow events (Safranyik 1985). During outbreaks, this insect can cause sustained mortality over a number of years, sometimes

leading to drastic species conversion and change of stand age structure (Schmid and Frye 1977). The effect is a release of suppressed trees similar to that observed following selective harvesting of overstorey spruce (Veblen *et al.* 1991, Lindgren and Lewis 1997). These effects are most pronounced in stands with a homogeneous, spruce-dominated canopy. In heterogeneous stands, only the larger spruce trees are successfully attacked, resulting in a less patch-like disturbance event. Due to the influence of aggregation pheromones, which are species-specific chemicals produced by the bark beetles to aggregate, attacks on single trees can often spill over to adjacent trees (Borden 1982). In heterogeneous stands, the likelihood of such spill over is lower because the large susceptible spruce trees are generally spaced further apart, and the impact of outbreaks is generally much less severe (Lewis and Lindgren 2000). From an ecological point of view, the long-term impacts of a moderate outbreak on a stand may be small. From the point of view of forest management, however, even moderate spruce beetle-caused mortality leads to considerable loss in timber volume, given that a relatively small proportion of large diameter spruce would contribute a large portion of the harvestable volume in the stand.

The effect of spruce beetle on stand structure is such that heterogeneity tends to increase following outbreak (Veblen *et al.* 1991) and susceptibility of the stand decreases. In the absence of stand-replacing fire or spruce beetle outbreak, decay fungi may maintain stand heterogeneity. In stands where root disease or other mortality agents act selectively on subalpine fir, spruce dominance may increase over time. This leads to significant impact when spruce beetle populations build up (Lindgren and Lewis 1997, Lewis and Lindgren 1999), which may have a patch initiation-like effect on the stand.

Fine-scale processes within the SBS and ESSF

Fine-scale disturbance agents influence forest dynamics through single and small-group mortality, and the pattern and frequency of mortality differs with disturbance agent. With increasingly greater time periods between stand replacing events, fine-scale disturbances, caused by biotic and abiotic agents, maintain and renew the forest structure in stands with long fire-return intervals (Lewis and Lindgren 1999, Newbery 2001).

Fine-scale disturbance patterns and processes have been characterized within tropical forests (Denslow 1987, Lawton and Putz 1988), temperate North-American forests (Frelich and Graumlich 1984, Runkle 1984, Lorimer *et al.* 1988, Lorimer and Frelich 1989, Payette *et al.* 1990, Abrams *et al.* 1995), eastern sub-boreal forests (Frelich and Reich 1995), western coastal forests (Canham 1988, Lertzman *et al.* 1996, Brett and Klinka 1998) and western subalpine forests (Lertzman and Krebs 1990, Lertzman 1992, Lundquist and Beatty 2002). Although there is an emerging body of literature suggesting that fine-scale disturbances are an important element of boreal and sub-boreal forest structure (McCarthy 2001), little is known about fine-scale disturbance regimes in the SBS and ESSF biogeoclimatic zones found in central and east-central British Columbia. Further, much of the work on fine-scale disturbance has been dedicated to describing gap structure and tree regeneration dynamics within and around canopy gaps (White and Mackenzie 1985, Yamamoto 1995, Kneeshaw and Bergeron 1998), and not the agents of gap formation. There is increasing evidence that insects, disease, and abiotic agents collectively play a significant role in gap formation (Dickman and Cook 1989, Hennon 1995, Lewis and Lindgren 1999), but these various gap-forming agents do not necessarily result in identical gap structure and function. The following sections review three of the most common fine-scale disturbance agents within the central interior of British Columbia.

Decay fungi

Many decay fungi can directly or indirectly cause tree mortality. Normally, decay fungi weaken the roots and/or the bole to such an extent that breakage occurs. Root and butt rots are some of the most important gap-making agents in sub-boreal and related forest types (Veblen 1986, Worrall and Harrington 1988, Holah *et al.* 1993, Hennon 1995, Lewis and Lindgren 1999), and therefore, are major contributors to processes that maintain heterogeneity of stand structure and composition.

Due to decay resistance of sapwood of living trees, decay fungi are often limited to the heartwood, or areas of dead or injured sapwood. Access to the heartwood by decay fungi occurs through natural openings, such as branch stubs (true heart rots), and through wounds (wound-entry heart rots). It takes years from the time of infection for extensive decay to develop. Therefore, the prevalence of decay fungi usually increases with stand age, becoming most evident only in older forest stands (Wagener and Davis 1954, Pothier *et al.* 2004).

Wound-entry heart rot fungi are numerous and usually have broad host ranges that include many members of particular tree families (e.g., Pinaceae). Many of these fungi are saprotrophs with a limited ability to decay wood in living trees. For example, *Fomitopsis pinicola* (Sw.:Fr) P. Karst is one of the most important decay fungi of dead coniferous wood, but in boreal ecosystems, it is also known as a wound-entry heart rot (Etheridge 1973).

Decay fungi generally cause breakage of individual trees, although broken trees may knock over or substantially damage other trees, such that a gap will expand over time (Hennon 1995). These gaps contribute to structural and species heterogeneity typical of old-growth forests in sub-boreal and subalpine forests.

Tomentosus root disease

Inonotus tomentosus (Fr.:Fr) S. Teng. is the dominant root pathogen in spruce-dominated boreal and sub-boreal ecosystems of B.C. This fungus attacks a broad range of conifer hosts, but is most frequently found on spruce and pine species. Hardwood species are thought to be immune to *I. tomentosus* (Whitney 1962, Whitney and Bohaychuck 1976).

Inonotus tomentosus causes gradual dysfunction of the root system; eventually the tree dies standing or is windthrown. The disease occurs in small clumps (2-3 trees) that gradually coalesce into larger areas of infected trees. Therefore the effect on stand structure depends on the incidence of root disease. At low levels it causes occasional gaps, but at higher levels (e.g., >20 % spruce infected) *I. tomentosus* creates greater structural and compositional diversity in the forest by causing small openings. Over time, *I. tomentosus* can cause a species shift to sub-alpine fir or other resistant species, or a more open, brushy stand structure (Whitney 1962). Root diseases are often considered to be diseases of the site. Once established in an area, they persist from one generation to the next and result in different processes occurring on infected sites than would occur without root disease. VanderKamp (1991) has termed this condition a root disease climax.

Tomentosus root disease also interacts with other agents of disturbance. It is thought to predispose trees to attack by root collar weevils (Cerezke 1994) and other agents that are more successful on stressed trees. Recent work has indicated that at endemic population levels, spruce beetles are more successful when they attack trees with low to moderate levels of root disease. At outbreak levels, there was no difference in attack success between healthy and infected trees (Lewis and Lindgren 2002). Therefore, tomentosus root disease can be an important stand structural and compositional modifier. It also influences population

dynamics of spruce beetle, another late-successional modifier that has varying effects on the forest depending on population size.

Western balsam bark beetle

Western balsam bark beetle, *Dryocoetes confusus* Swaine is an example of an insect that can cause either fine-scale disturbances, or intermediate- to coarse-scale (patch) disturbances. Western balsam bark beetle is widespread in British Columbia wherever subalpine fir grows (Garbutt 1992). Mortality caused by this beetle can be widespread and severe, but is generally scattered over large areas and outbreaks are sustained for many years (Stock 1991). Harder (1998) observed that attacked trees were found disproportionately in larger diameter classes. Bleiker *et al.* (2003) found that successfully attacked trees had reduced growth rates in the last 10 years relative to unattacked trees, indicating that this insect prefers declining trees. Subalpine fir is subject to many mortality agents, and it has been speculated that species-specific mortality agents prevent this species from displacing spruce in many areas (Lewis and Lindgren 1999). The western balsam bark beetle appears to contribute to the turnover rate, but rarely becomes the driving force.

Conclusions

Within the mature, spruce-subalpine fir forests of central British Columbia the effects of fine- to coarse-scale disturbance agents can coincide at several temporal and spatial scales. As the time between stand-replacing events lengthens, the influence of fine-scale disturbance on stand structure and dynamics should increase. Despite the simplicity of the hypothesis, little is known about the fine-scale components of the disturbance regimes within the sub-boreal and subalpine ecosystems of central British Columbia. To characterize the fine-scale

disturbance regimes in any region, the legacy of past intermediate- and coarse-scale disturbance events, and regional climate fluctuations, must be documented and partitioned as a source of variation controlling stand dynamics. The following chapters are intended to stand alone as separate manuscripts; however, together they are intended to assess the above hypothesis by quantifying and characterizing fine-scale disturbance patterns and processes as they vary across distinct sub-boreal and subalpine ecosystems of central British Columbia.

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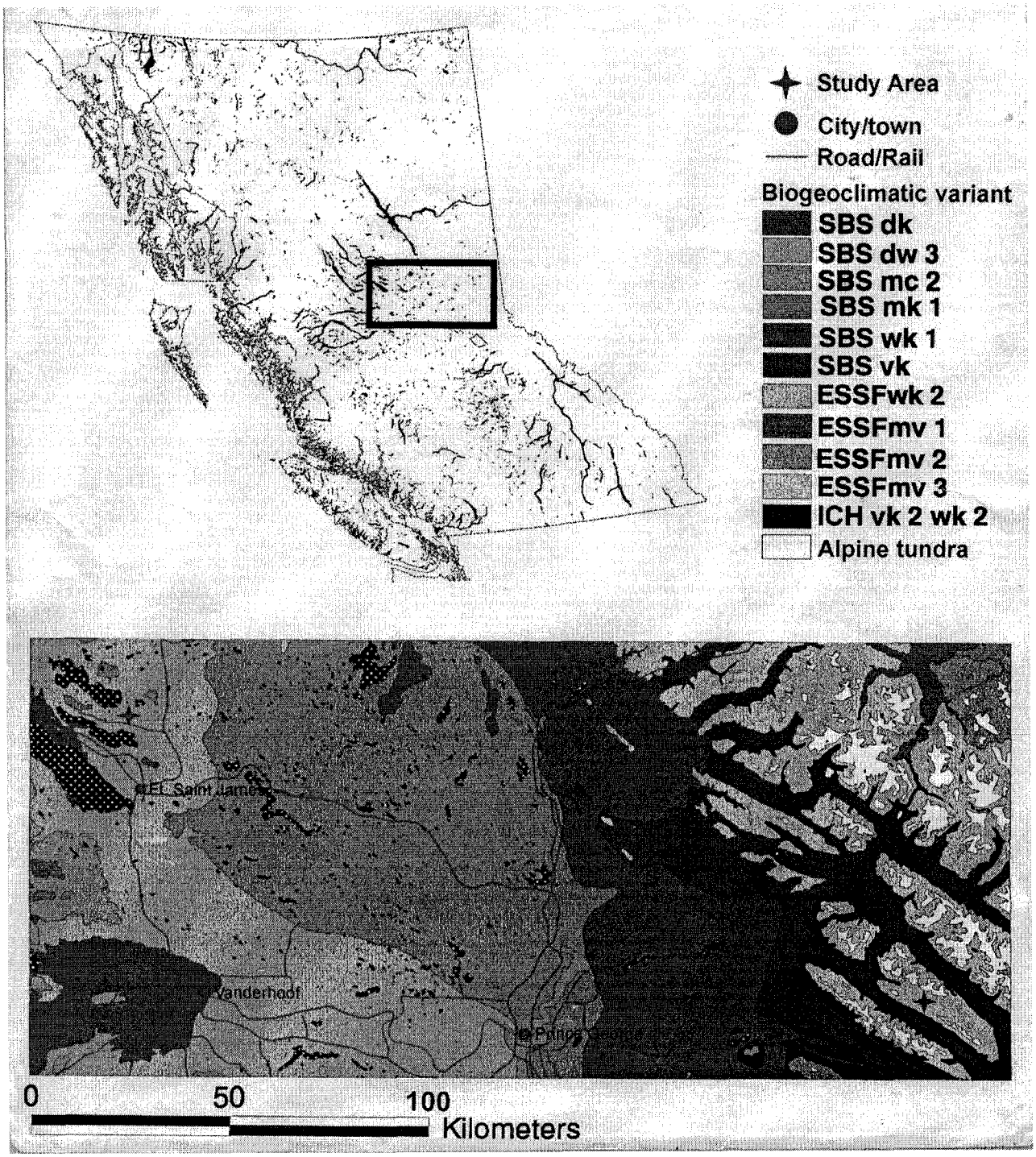

Figure 1.1. Locations of the Sub-Boreal Spruce and the Engelmann Spruce-Subalpine Fir biogeoclimatic zones and study areas.

CHAPTER 2 - DETECTING STAND AND LANDSCAPE-LEVEL DYNAMICS WITHIN MATURE SPRUCE-SUBALPINE FIR FORESTS OF CENTRAL BRITISH COLUMBIA: DENDROECOLOGICAL CONSIDERATIONS I

Abstract

This study used dendroecological techniques to examine the influence of past intermediate- and coarse-scale disturbance events, and regional climatic variation, on tree growth and stand development. As part of a larger project intended to characterize fine-scale disturbance in central British Columbia, three forested ecosystems were selected: dry sub-boreal, mesic sub-boreal and wet subalpine. Within each ecosystem, five 0.25-ha plots were located in mature spruce-subalpine fir stands (n = 15). Within each plot, increment cores were collected at breast height from all living and dead trees ≥15 cm diameter at breast height (dbh), species was tallied and dbh recorded. Cores were mounted, sanded, aged and ring-width series measured to the nearest 0.01 mm. Two standardization techniques were used to identify disturbance and infer climatic variation at scales greater than the individual plot. In the first standardization method, used to highlight long-term growth trends (e.g., spruce beetle outbreaks or stand-replacing fire), all series were transformed by dividing the observed ring-widths by each series' mean ring-width, and then averaged by species and by plot (n = 30). In the second standardization method, used to highlight short-term growth trends (e.g., climate), all series were transformed by fitting a cubic-smoothing-spline of 50 % frequency response of 50 years, and then averaged by species and by plot (n = 30). Periods of canopy mortality occurred in the ESSFwk1 variant during the 1710s and 1830s, in the SBSwk1 variant during the 1830s and 1870s, and in the SBSdw3 variant during the 1870s. Based on historical documentation and dendroecological evidence, these periods of canopy mortality

were likely caused by spruce beetle. There is strong evidence that these events caused abrupt shifts in species composition. A western balsam bark beetle outbreak occurred in the ESSFwk2 variant during the 1920s and 1930s. Dendroecological evidence provides strong evidence that species dominance shifted abruptly from subalpine fir to spruce within these stands. The results of this study clearly demonstrate that dendroecological techniques can be used to date and examine the effects of past intermediate- and coarse-scale disturbance events and regional climate fluctuations. Furthermore, these events can have a significant influence on tree-growth and stand development, and therefore should be taken into consideration before estimating fine-scale disturbance frequencies.

Introduction[1]

The sub-boreal and subalpine forest ecosystems of central British Columbia have been receiving greater attention with regard to their natural disturbance regimes (Andison 1996, DeLong and Tanner 1996, Hawkes *et al.* 1997, DeLong 1998, Newbery 2001, Sanborn *et al.* 2001). Historically, stand-replacing fire was considered the primary disturbance agent controlling stand and landscape-level dynamics (Johnson 1992, Andison 1996, DeLong and Tanner 1996, Hawkes *et al.* 1997, DeLong and Kessler 2000). Although in most cases these forests do originate following fire, recent studies have shown that the times between stand-replacing events are enormously varied. For example, DeLong and Tanner (1996) reported fire-return intervals ranging from 227-345 years in drier forest types in the foothills of the Rocky Mountain. Hawkes *et al.* (1997) report fire-return intervals in extremely wet and cool forest types in the central Canadian Rocky Mountains ranging from 1200-6250 years.

Two major problems occur when defining the disturbance regime of a forested ecosystem exclusively by the disturbance agents that cause stand-replacement over coarse spatial scales (e.g., coarse-scale fire in boreal ecosystems). First, disturbance events are not strictly coarse-scaled, stressing and/or causing the death of the majority of canopy trees over large contiguous areas (White 1979). Disturbance events can be fine-scaled, causing single and small group mortality. Furthermore, the fine-scale components of a disturbance regime can be stand-maintaining as opposed to stand-replacing (Lewis and Lindgren 1999). Stand-replacing disturbance events typically promote stand-initiation, even-aged stand structure and shifts to early-seral species composition (Oliver and Larson 1996). Conversely, stand-

[1] A version of this document will be submitted for publication under multiple authors. All data used in this study were collected by R. D. Thompson and a number of field and lab assistants. In this thesis I use 'we' and 'our' to reflect the involvement of others in various aspects of this work.

maintaining disturbance events typically cause gap-formation, uneven-aged stand structure and the maintenance of late-seral species composition or slow shifts in species composition (Lewis and Lindgren 1999). The second problem occurs because a gradient between fine- and coarse-scale disturbance agents can exist, leading to intermediates between the fine- and coarse-scaled disturbance processes (Antos and Parish 2002). With increasing periods between stand-replacing events, fine- to intermediate-scale disturbance events are increasingly important in forest dynamics (Lewis and Lindgren 2000). These disturbances, caused by a collection of biotic and abiotic agents, and interactions between agents, can maintain and renew forest structure in stands with long fire-return intervals (Lewis and Lindgren 2000). Due to our traditional management and scientific focus on coarse-scale disturbance, however, little is known about these fine-scale disturbance processes. This is particularly true in wet temperate forests with long intervals between stand-replacing events. In order to advance our understanding of the disturbance regimes within the central interior of British Columbia, we must not focus solely on coarse-scale processes, but include the characterization of fine-scale processes and determine their relative importance in maintaining ecosystem function and health.

Tree-ring patterns contain a wealth of information and dendroecological analyses offer the possibility of examining the effects of past climate, disturbance and competition on tree growth and stand development, provided that the effects of these factors can be disentangled (Parish *et al.* 1999). Within sub-boreal and subalpine forest ecosystems the effects of fine- to coarse-scale disturbance agents can coincide at several temporal and spatial scales (Parish *et al.* 1999, Lewis and Lindgren 2000). Furthermore, forested ecosystems in central British Columbia have been shown to be sensitive to climatic variation, and attempts have been made to reconstruct past climate to understand the specific growth-climate

relationships (Zhang *et al.* 1999). Therefore, we expect that the influence of disturbance and climate together produces a diversity of tree-ring growth responses. Furthermore, these signals can be complex and often inseparable (Parish *et al.* 1999).

To characterize the fine-scale disturbance regimes in any region, the legacy of past intermediate- and coarse-scale disturbance events, and regional climate fluctuations, must be documented. Our objectives were to develop size- and age-class distributions, and a set of stand- and regional-level chronologies, to diagnose past intermediate- and coarse-scale disturbance events and climatic fluctuations that have significantly influenced stand development. Subsequent chapters use the diagnoses of these events to aid in the reconstruction of individual stand histories and to compare and contrast stand structure, composition and dynamics in the mature spruce-subalpine fir forests of central British Columbia.

Materials and Methods

Field Sampling

We selected three biogeoclimatic variants to represent the climatic gradient that spans the dry-warm interior plateau to the wet-cold foothills of the Canadian Rockies (Chapter 1, Figure 1.1). The Stuart Dry Warm Sub-Boreal Spruce (SBSdw3), Willow Wet Cool Sub-Boreal Spruce (SBSwk1) and Misinchinka Wet Cool Engelmann Spruce-Subalpine Fir (ESSFwk2) biogeoclimatic variants are located in two of the most common biogeoclimatic zones located in central British Columbia. The SBSdw3, SBSwk1 and ESSFwk2 biogeoclimatic variants will be referred to as the dry, mesic and wet variants, respectively.

Within each variant, we selected five forest stands. Stands were selected using several criteria. First, forest stands were beyond the stem exclusion stage as defined by

Oliver and Larson (1996). This criterion was used to select stands in which trees were establishing in the understorey and, in the absence of stand-replacing disturbances, were advancing toward the true old-growth stage of development (Oliver and Larson 1996). Second, forest soils had intermediate soil moisture (mesic) and nutrient (mesotrophic) regimes (Meidinger and Pojar 1991). This criterion was intended to minimize variation in tree species growth characteristics and disturbance processes as a result of highly divergent edaphic influences of soil moisture and nutrients. Third, forest stands had a mixture of spruce and subalpine fir as the dominant component of the canopy, with basal area >80 %, for all trees over 15 cm diameter at breast height (dbh, measured 1.3 m above the ground). A common tree composition and density minimized variation in stand susceptibility to disturbance. Finally, forest stands had no evidence of industrial forest activities. This final criterion ensured that stand dynamics resulted from natural disturbances, which may include past traditional uses and practices of First Nations. Consequently, stands are not representative of the average of the biogeoclimatic variant, but rather, they are typical of stands satisfying the criteria within each variant.

Within each stand, one 0.25-ha plot was located by randomly placing the south-western plot corner, which was defined as the plot origin (0, 0 m), for a total of 15 plots. From the plot origin, plot boundaries were defined by a 50-m × 50-m closed traverse along each cardinal bearing. At each plot corner and traverse midpoint (i.e., 25 m), stakes were placed and numbered one to eight.

For all living and dead trees with dbh >15 cm, we mapped the x and y coordinates relative to the plot origin. All coordinates were calculated using two azimuths taken from any two adjacent stakes with a 25-m base and related back to the origin using trigonometry. Coordinates were used for revisiting each plot and spatial analyses in subsequent chapters.

Trees were numbered, species tallied and dbh measured. For all dead and downed material, with dbh >15 cm, dbh was recorded based on an estimate of breast height measured from the root collar and species was tallied if it could be determined based on bark characteristics. Diameter distributions were plotted for living spruce and subalpine fir, and for dead spruce, subalpine fir and the unidentifiable trees, separately for each plot. Differences in the diameter distributions were analyzed using Kruskal-Wallis single-factor analysis of variance by ranks (Zar 1996, SPSS Inc. 1999).

Dendroecological analyses

Increment cores were taken at breast height from each live and dead tree. Cores were taken at breast height because they tend to have less stem decay than cores taken lower on the stem enabling maximum length in ring-width series. Further, a large number of the dead trees in the study areas exhibited butt-rot which was largely avoided by coring at breast height. We only cored dead trees if the outer most tree ring corresponded to the last ring formed prior to tree death. We assumed that the outer ring was the last ring formed prior to tree death if the bark was intact and/or the sapwood was present and firm. Following the methods of Storaunet and Rolstad (2002), cross-sectional discs were collected from felled snags and logs if intact sapwood, on at least one portion of the tree, could be found and used to determine the date of death by cross-dating. Tree-ring series from disc samples were used to develop chronologies.

Cores were prepared following standard dendrochronology techniques (Stokes and Smiley 1968). Discs were frozen after field sampling and prepared and measured based on the methods of Herman *et al.* (1972). Individual ring-width series were measured to the nearest 0.01 mm using WinDENDRO (Regent Instruments Inc. 2000). For discs and cores

that had periods of extremely narrow ring-widths (individual rings ≤0.5 mm wide) the ring-width series were measured to the nearest 0.001 mm using the Velmex "TA" System (Velmex, Inc. 1992) in conjunction with MeasureJ2X (VoorTech Consulting 2004).

Ring-width series were cross-dated by matching the ring-width patterns among samples from live and dead trees. Cross-dating assures the proper placement of calendar years to each growth ring and identifies missing, partial, locally absent and false rings (Fritts 1976). We used the computer program COFECHA (Holmes 1983) and visually inspected the samples to detect measurement and cross-dating errors. Once the ring-width series were dated, frequency distributions of age at breast height were plotted for living spruce and subalpine fir, separately for each plot. Disc samples were not used to develop age-class distributions because they were not necessarily taken from breast height. A few core samples did not include the pith; therefore, the number of missed rings was calculated as the estimated distance to the pith divided by the mean ring-width of the first five complete rings.

Standardization is a common technique used to estimate and remove systematic variation in individual ring-width series that is not associated with an environmental signal of interest (Cook and Peters 1981, Cook 1987). A signal is defined here as the information in tree rings which is relevant to the study of a particular problem (Cook 1987). Standardization involves fitting the observed ring-width series with a predictive function and computing an index by dividing the observed value by the predicted value. This reduces variance among series and transforms individual ring-widths into dimensionless index values. Standardization permits computation of average ring-width chronologies without the average being dominated solely by faster growing trees with large ring widths (Veblen *et al.* 1991b).

Two standardization techniques were used to identify unique disturbance and climatic events at scales greater than the individual plot. In the first, horizontal-line standardization,

all cross-dated series were transformed by dividing the observed ring width by the mean series ring width. Veblen *et al.* (1991b) found that standardizing series by their mean preserved long-term growth trends and could be used to identify canopy disturbance. Using the program ARSTAN (Cook and Holmes 1984) individual series were standardized and averaged by species and by plot (n = 30). These chronologies were used to: (1) date partial canopy removal severe enough to register within a majority of the existing canopy trees; and (2) reveal tree growth patterns that indicate stand-replacement events. Dating events associated with stand-replacement and partial canopy removal will be used to assist in the differentiation between these typically coarse- and intermediate-scaled events from more fine-scaled processes.

The goal of the second standardization was to develop a set of chronologies from which we could interpret short-term growth trends. Included in this category would be defoliator cycles, inter-annual and short-term intra-annual variations in climate. Fine- to coarse-scale disturbance events are common in the spruce-subalpine fir forest types of central British Columbia, and plots were selected to sample disturbance effects rather than to highlight the year-to-year climate variation. We evaluated numerous methods of standardization and found the strongest estimates of the short-term population signal using stochastic opposed to deterministic methods (Cook, 1987). Using the program ARTSAN (Cook 1985) ring-width series were standardized by fitting a cubic-smoothing spline of 50 % frequency response of 50 years and averaged by species and by plot (n = 30).

Marker-ring analysis, within- and between-species correlations, and principal component analysis (PCA) were used to assess individual cubic-spline chronologies within each ecological variant. Wide and narrow marker rings that are temporarily synchronous among chronologies suggest a common influence on tree growth (Daniels and Watson 2003).

We defined marker rings as years when the normalized ring-width indices of the standard chronologies were more than one standard deviation from the chronology mean. The degree of commonality of these positive and negative marker rings was assessed by examining the percentage of chronologies showing marker rings in each year. Years when greater than 60 % of the chronologies had a marker ring of the same sign were considered common (Daniels and Watson 2003).

Within-species correlation matrices were calculated for each of spruce and subalpine fir in each ecological variant (2 species × 3 ecological variants = 6 matrices) (SPSS Inc. 1999). Each pair-wise matrix correlates the five species-specific chronologies against one another resulting in 10 unique r values per matrix. Between-species correlation matrices were calculated for each ecological variant (SPSS Inc. 1999). Each pair-wise matrix correlates each spruce chronology against each subalpine fir chronology resulting in 25 unique r values per matrix.

Separate PCA, using varimax rotation, were run for each ecological variant (SPSS Inc. 1999, Tabachnick and Fidell 2001). PCA analyses were conducted over the common pair-wise intervals for the 10 chronologies within each ecological variant. If species respond differently to climatic variation then the PCA should group the chronologies accordingly.

Results

Diameter and age structure at breast height

Diameter distributions of living spruce and subalpine fir varied between plots within and between each ecological variant (Figure 2.1). Within the dry variant, plots 1 and 2 were dominated by subalpine fir in the smallest size-classes and plots 3 and 4 were dominated by spruce in the smallest size-classes. Plots 1 and 2 are at a latter stage of stand development

based on the ingress of subalpine fir into smaller size-classes, and the flatter distribution and lower density of spruce relative to subalpine fir. Plot 5 represents an intermediate stage of stand development between the two pairs, respectively (Figure 2.1). All plots in the mesic variant were similar to plots 1 and 2 of the dry variant, and all plots in the wet variant were similar to plots 3 and 4 of the dry variant (Figure 2.1). In the mesic variant, spruce had flatter distributions (Figure 2.1) and consistently larger maximum diameters compared with subalpine fir ($\chi^2 = 6.818$, df = 1, $p < 0.01$, Figure 2.1). In contrast, subalpine fir was more abundant in smaller size-classes compared with spruce within the mesic variant (Figure 2.1). Within the wet variant, the diameter distributions of both spruce and subalpine fir formed a reverse-J; however, spruce had larger maximum diameters than subalpine fir ($\chi^2 = 6.818$, df = 1, $p < 0.01$, Figure 2.1).

Within the dry variant, plots are primarily single cohort stands (Figure 2.2). Plots 1 and 2 have dominant subalpine fir cohorts at approximately 130 years breast height age, with residual spruce and fir up to 270 years. Plots 3, 4 and 5 all have dominant spruce cohorts with approximately 110-130 years breast height age, with a few residuals up to 210 years. Together, these observations provide further evidence that plots 1 and 2 within the dry variant are at a latter stage of stand development than plots 3, 4 and 5. Within the mesic variant, plots range from 50 to 250 years at breast height. Plots 1 and 3 have a bimodal distribution of breast height ages with subalpine fir around 110 years and spruce around 230 years. Plots 2, 4 and 5 have multimodal distributions of breast height age with old spruce and one or two younger influxes composed of spruce and/or subalpine fir. Within the wet variant, most trees are <170 years old at breast height, with a few residuals up to 300 years old. In plot 3, most spruce attained breast height 130 to 150 years ago and in the remaining plots spruce and subalpine fir attained breast height 50 to 150 years ago (Figure 2.2).

The general form of the diameter distributions of dead spruce, subalpine fir and unidentifiable trees varied in plots within and among each ecological variant (Figure 2.3). Within the dry variant, the dead tree diameters from plots 1 and 2 are greater than plots 3, 4 and 5 ($\chi^2 = 107.8$, df = 1, $p < 0.001$). Plots 1 and 2 were dominated by subalpine fir in the smallest size-classes and plots 3 and 4 were dominated by spruce in the smallest classes. Within plot 5, subalpine fir dominated the smallest size class and spruce dominated in the larger size-classes. Similar to the live tree diameter distributions, plot 5 represents an intermediate stage of stand development between plots 1 and 2, and plots 3 and 4. Furthermore, plots 1 and 2 are indicative of a latter stage of stand development based on the greater abundance of unidentifiable trees in all size-classes and the abundance of spruce and subalpine fir larger size-classes. All plots in the mesic variant were similar to plots 1 and 2 of the dry variant. All plots in the wet variant, although similar to plots 3 and 4 of the dry variant with regard to their size-class distributions of dead spruce and subalpine fir, had a larger component of trees without bark, indicating a later stage of stand development.

Ring-width chronologies

All chronologies have a maximum sampling depth >20 trees and 90 % of the chronologies have starting dates >200 years before present (Table 2.1). Furthermore, 93 % of the chronologies have mean between-tree correlations >0.40 (Table 2.1). The maximum sampling depths, chronology start dates and mean correlations for all 30 chronologies, using horizontal standardization, suggest that adequate replication was attained to detect radial growth patterns indicative of stand-replacement and/or partial canopy removal.

Of the five plots in the dry variant, the chronologies from plots 1 to 2 included a period in which spruce showed increased growth, possibly the result of a sand-replacing

event (Figure 2.4). Based on the limited sampling depths during these periods, however, it is difficult to place accurate dates on stand-replacement. Similarly, all of the chronologies in the mesic variant indicate an initial period of rapid growth (Figure 2.4). In contrast to the dry and mesic variants, the majority of the chronologies in the wet variant do not indicate an initial period of rapid growth (Figure 2.4).

Within the dry variant, the chronologies of plots 1 and 2 have a minor sustained increase in index values after the 1870s (Figure 2.4). Within the mesic variant, all plot chronologies also show a similar pattern during the 1830s and 1870s (Figure 2.4). Within the wet variant, there are three periods of increased index values: the first period of increase in the 1710s; the second increase in the 1830s; and the third in the early 1930s (Figure 2.4).

Across all ecological variants, the chronologies using cubic-spline standardization included 21 to 54 cores and spanned at least 159 years (Table 2.2). In all variants, the mean chronology length was consistently longer for spruce compared with subalpine fir (Table 2.2). The mean sensitivity and standard deviation values provide a measure of the year-to-year variability in the chronologies (Fritts 1976). The average mean sensitivities, standard deviations and first-order autocorrelations for the spruce chronologies within the dry, mesic and wet variants are similar to the shorter subalpine fir chronologies (Table 2.2). The expressed population signal (EPS) is a measure, based on a finite number of samples, of how well a chronology approximates the theoretical population (Cook and Kariukstis 1990). This is related to the strength of the common signal and sample replication. Mean correlation between trees values (r_{bt}) also serve as a preliminary and conservative estimate of the common signal in the chronologies. The number of trees required to attain an EPS of 0.85 has been suggested as desirable for approximating a common signal within the theoretical population (Briffa 1995, Briffa and Jones 1990). The mean correlations for spruce

chronologies within the dry, mesic and wet variants (0.44, 0.47 and 0.45, respectively) indicate that, on average, seven or eight samples are required to yield the suggested EPS (Table 2.2). Correlations for subalpine fir within dry, mesic and wet variants (0.42, 0.44 and 0.37, respectively) indicate that, on average, eight to thirteen samples are required to yield the suggested EPS (Table 2.2). The greater number of samples required for subalpine fir within the wet variant, implied by the lower r_{bt}, may suggest that the subalpine fir populations respond differently and more variably to climate and past disturbance (Table 2.2). In all ecological variants, there are a number of years where greater than 60 % of the chronologies have common marker rings suggesting that the chronologies possibly have a common climate related signal within each variant (Figure 2.5).

Eighty-five percent of the correlations over the maximum pairwise intervals exceeded 0.4 and 98 % of the correlations were significant ($p < 0.05$). Except for a few pairs, all correlations were strong with a mean of 0.62 ($n = 60$). Seventy-nine percent of the correlations over the maximum pairwise intervals exceeded 0.4 and 88 % of the correlations were significant ($p < 0.05$). Again, except for a few pairs, all correlations were quite high with a mean of 0.49 ($n = 75$).

Within the dry variant, two components where identified by the PCA and accounted for 82 % of the variance within the 10 chronologies (Table 2.3). These components were retained and subjected to an orthogonal varimax rotation. The loadings on the two components grouped the spruce and subalpine fir of plots 3, 4 and 5 and the spruce and subalpine fir of plots 1 and 2, suggesting distinct differences in group responses to cubic-spline standardization and variation in stand dynamics. Within the mesic variant, two components accounted for 81 % of the variance within the 10 chronologies (Table 2.3). The loadings identified two groups with the subalpine fir of plot 3 separate from all other

chronologies. Within the wet variant, two components accounted for 84 % of the variance within the 10 chronologies (Table 2.3). The loadings identified two groups with all chronologies loading together except for the subalpine fir chronologies of plots 1, 2 and 4.

The above analyses, along with an examination of the co-located chronologies (Figure 2.6), suggest common ring-width variability. Based on the spatial scale of these chronologies, it is justifiable to assume that the common variability between the two species is controlled by a common climatic factor at a regional scale. Disturbance histories, however, have resulted in important differences between species and between plots, especially within the dry variant. Subsequent analysis of short-term variation in the chronology dataset, therefore, should include mean regional chronologies for each species. In addition, based on these analyses, the dry variant requires further separation into two groups based on the differences in stand development. Plots 1 and 2 and plots 3, 4 and 5 will be combined into groups representing late and early-successional stages, respectively.

Eight final cubic-spline chronologies have been built for spruce and subalpine fir within the central interior of British Columbia (Table 2.4 and Figure 2.7). ARSTAN first order autocorrelations (Cook 1985) within the final chronologies were strong, suggesting that ring-width values are highly autocorrelated with the previous ring-width (Table 2.4). Therefore, post-hoc analyses of extended periods of below and above average growth should not include 2-year periods. Consequently, below average growth was defined as index values <1 for ≥ 3 consecutive years. There were no significant differences in the duration of below average growth across the ecological variants ($F_{3,4} = 5.71$, $p = 0.063$) and there were no significant differences in the duration of below average growth between spruce and subalpine fir nested within ecological variant ($F_{4,90} = 0.441$, $p = 0.779$). Mean duration of below average growth was four years and ranged from 3-16 years. The duration of above average

growth, defined as index values ≥1 for ≥3 consecutive years, were not significantly different by ecological variant ($F_{3,4} = 0.115$, $p = 0.947$) or by species nested within ecological variant ($F_{4,95} = 1.604$, $p = 0.179$). Mean duration of above average growth was five years and ranged from 3-13 years.

Discussion

The results of this study clearly demonstrate that dendroecological techniques can be used to date and examine the legacy of intermediate- and coarse-scale disturbance events and regional climate fluctuations within the mature spruce and subalpine fir forest types of central British Columbia. Furthermore, the two standardization procedures used within this study suggest that intermediate- and coarse-scale disturbances and variation in climate have a substantial influence on tree-growth and stand development, and should be taken into consideration before characterizing fine-scaled disturbance regimes in these forests. Without doing so, the above factors of tree-growth, that have the potential to cause growth patterns that are similar to fine-scale disturbance events, may go undetected. Additionally, estimated rates of fine-scale disturbance may be inflated due to intermediate- and coarse-scaled events not accounted for.

Standardization with a horizontal line passing through the mean ring-width value is meant to preserve long-term growth trends that characterize stand dynamics as a whole. At the beginning of each chronology, the above-average radial increment of spruce is indicative of open conditions and provides evidence for stand-replacement. Below-average growth followed by a dramatic and sustained increase in growth would provide evidence for partial canopy removal (Veblen *et al.* 1991a). With few exceptions, all plots within the dry and mesic variants indicate open conditions during the earliest periods of their chronologies

(Figure 2.4). The lack of an initial period of increased growth in spruce in plots 2 and 5 within the wet variant suggests that these plots are older than the earliest periods represented in the chronologies. Small sample depths, however, limit the strength of interpretation of these early periods. Veblen *et al.* (1991a) found that the pattern of release caused by spruce beetle outbreaks was usually evident with as few as five samples, but it is desirable to have at least 15-20 samples to assure adequate replication. If this guideline for sample size is transferable to the detection of growth patterns after stand-replacement, it becomes difficult to state with any veracity whether the periods of rapid early growth indicate stand-replacement or a host-specific disturbance agent that is represented by gap-origin samples alone. For example, plots 4 and 5 within the dry variant and plots 2 and 5 within the wet variant show below average growth in the earliest periods of their chronologies, followed by release and a prolonged period of sustained above average growth. These periods, however, are represented by fewer than five samples (Figure 2.4).

Without detailed historical records, stand-replacement and partial canopy removal can be difficult to differentiate. A number of non-dendrochronological methods and historical records were, therefore, used to make the distinction between these two disturbance types. In addition, shifts in age at breast height and diameter distributions for each species are both useful tools used to detect past beetle outbreaks and to distinguish their effects from coarse-scale wildfire (Veblen *et al.* 1991a). For example, within the wet and mesic variants, and plots 1 and 2 of the dry variant, bimodal or multimodal distributions of breast height ages indicate pulses in which spruce and subalpine fir attained breast height (Figure 2.2).

Insects have played an important role in opening the canopy of mature, spruce subalpine fir stands (Schmid and Frye 1977, Holsten 1990). In central British Columbia, observations made by McLean (1849) and the dendroecological evidence provided by

Lindgren and Lewis (1997) and Zhang *et al.* (1999) suggest that a spruce beetle outbreak occurred in the 1830s. No written historical records support spruce beetle outbreak in the other periods. Newbery (2001), however, studying the influence of *Inonotus tomentosus* (the causal agent of tomentosus root disease) on stand structure and dynamics within sites similar to the plots within the mesic variant of this study, found a slight increase in the frequency of trees that originated in gaps and releases from suppression during the 1870s through to the 1890s. A western balsam bark beetle outbreak substantially reduced the proportion of subalpine fir within all wet variant plots during the 1920s and 1930s, and beetle galleries are still abundant within these plots (R. D. Thompson, UNBC, unpublished data). A similar disturbance, caused by western balsam bark beetle, was identified during the 1930s in the Caribou Plateau in southeastern British Columbia (Koot and Hodge 1992, Parish *et al.* 1999). The bark beetle outbreak identified within our study resulted in the recruitment of live spruce and subalpine fir into smaller diameter-classes (Figure 2.1), a large number of dead subalpine fir in the smaller diameter-classes (Figure 2.3) and a pulse of spruce and subalpine fir recruitment after the 1920s and 1930s (Figure 2.2). This beetle outbreak provided opportunities for spruce and subalpine fir to achieve breast height. In recent periods, a similar pattern was evident within plots 1, 2 and 5 of the dry variant and within plots 1, 3, 4 and 5 of the mesic variant. Within these plots, a large number of dead subalpine fir in smaller diameter-classes (Figure 2.3) and abundant diagnostic signs (i.e., beetle galleries) suggests that western balsam bark beetle is currently reducing the proportion of subalpine fir within the canopy (R. D. Thompson, UNBC, unpublished data). Based on this evidence alone, however, it is too early to suggest that spruce is recruiting into the canopy.

The second standardization procedure, which identified short-term variations in growth that are primarily used to study climate-related growth patterns, suggests that spruce

and subalpine fir exhibit moderate dendroclimatic utility. Compared with other coniferous species in the interior of British Columbia, mean sensitivity and standard deviation values for spruce and subalpine fir tend to be lower (Zhang *et al.* 1999, Watson and Luckman 2001, Watson and Luckman 2002, Daniels and Watson 2003, Wilson and Luckman 2003). In addition, the number of samples required for spruce and subalpine fir to attain the recommended EPS is slightly greater, reflected by the lower correlation between trees (Zhang *et al.* 1999, Watson and Luckman 2001, Watson and Luckman 2002, Daniels and Watson 2003, Wilson and Luckman 2003). PCA analyses suggest that variation among the chronologies is related to disturbance histories and not necessarily to differences in each species' response to climate. This also suggests that a generalization of the regional climate signal is possible; however, separate species/regionally-specific chronologies would be necessary because of partial canopy removal caused by the host-specific disturbance agents identified above (i.e., spruce beetle and western balsam bark beetle).

A major objective of this study, however, was not to reconstruct climate, but to develop chronologies that identify periods where below and above average growth rates may appear similar to patterns caused by disturbance. The duration of climate-related growth patterns are key factors used to distinguish disturbance events from climatic variation. Within the central interior of British Columbia the mean duration of below and above average growth were 4 and 5 years and ranged from 3-16 and 3-13 years, respectively. In rare cases, below average growth followed by above average growth (or simply the return to average growth) could result in regionally synchronous patterns in the majority of canopy trees that appear as growth releases, but are not related to disturbance. Within the dry variant chronologies, one such event occurred during the 1960s (Figure 2.7) and is of concern regarding future estimation of fine-scale disturbance frequencies. A comparison of the dry

variant chronologies in Figures 2.4 and 2.7 suggests that the pattern is linked to climate because no sustained release patterns were apparent in the horizontal line standardized chronologies for any of the dry variant plots during the same decade.

In conclusion, an accurate identification of growth patterns related to intermediate- and coarse-scale disturbance and climate, and their overall effects on stand development, enable greater confidence in the identification of growth patterns associated with fine-scale disturbance. Further, dendroecological techniques contribute to characterizing natural disturbance. These techniques, however, need to be matched by non-dendroecological methods such as the examination of diameter distributions for living and dead samples, shifts in species composition through time, spatial analyses of disturbance, and the quantification of unique disturbance agents that brought about the diverse histories within each stand.

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Table 2.1. Summary statistics for the 30 species- and plot-specific chronologies. Chronologies were standardized using a horizontal line.

Variant	Species	Plot	N	Chronology starting date	Mean correlation
Dry	**Spruce**	**1**	39	1724	0.49
		2	27	1710	0.40
		3	88	1862	0.79
		4	86	1805	0.80
		5	58	1869	0.81
	Subalpine fir	**1**	67	1777	0.48
		2	86	1771	0.55
		3	26	1799	0.72
		4	31	1811	0.77
		5	59	1795	0.68
Mesic	**Spruce**	**1**	38	1748	0.53
		2	41	1769	0.49
		3	48	1706	0.58
		4	44	1766	0.53
		5	28	1761	0.55
	Subalpine fir	**1**	52	1769	0.47
		2	77	1763	0.67
		3	85	1791	0.51
		4	67	1741	0.62
		5	87	1784	0.55
Wet	**Spruce**	**1**	67	1623	0.66
		2	68	1633	0.62
		3	76	1614	0.60
		4	62	1658	0.61
		5	69	1649	0.54
	Subalpine fir	**1**	59	1732	0.33
		2	51	1690	0.39
		3	40	1741	0.68
		4	47	1712	0.50
		5	58	1649	0.42

Table 2.2. Mean summary statistics for the species- and site-specific chronologies. Chronologies were standardized using a cubic spline. Mean length is the mean length of all cores in a chronology. Mean sens., Std. dev., and AC(1) are mean sensitivity, standard deviation and first order autocorrelation, respectively. Mean r_{bt} is the mean correlation between trees. Trees EPS 0.85 is the number of trees required to attain an expressed population signal (EPS) value of 0.85.

Variant	Species	No. Cores	Start	Range in Length (yrs)	Mean Length (yrs)	Mean sens.	Std. dev.	AC(1)	Mean r_{bt}	Trees EPS 0.85
Dry	**Spruce**	54	1818	134 - 230	185	0.14	0.18	0.53	0.44	8
	Subalpine fir	29	1843	115 - 209	160	0.13	0.19	0.59	0.42	8
Mesic	**Spruce**	21	1770	206 - 251	233	0.15	0.21	0.59	0.47	7
	Subalpine fir	50	1821	136 - 229	182	0.18	0.26	0.59	0.44	8
Wet	**Spruce**	53	1775	157 - 388	228	0.15	0.20	0.49	0.45	8
	Subalpine fir	20	1844	95 - 225	159	0.15	0.23	0.55	0.34	13

Table 2.3. Summary statistics for the principal component analyses (PCA). Components were subjected to a varimax rotation. Bold values identify the highest loading for each chronology.

Variant	Species	Plot	PC1	PC2
Dry	**spruce**	**1**	0.22	**0.91**
		2	0.34	**0.87**
		3	**0.85**	0.31
		4	**0.85**	0.37
		5	**0.72**	0.48
	subalpine fir	**1**	0.26	**0.87**
		2	0.26	**0.88**
		3	**0.86**	0.05
		4	**0.86**	0.23
		5	**0.81**	0.40
		% of variance	65.4	16.5
Mesic	**spruce**	**1**	**0.83**	-0.04
		2	**0.92**	0.14
		3	**0.83**	0.12
		4	**0.91**	0.11
		5	**0.91**	0.08
	subalpine fir	**1**	**0.65**	0.61
		2	**0.69**	0.58
		3	-0.17	**0.88**
		4	**0.80**	0.48
		5	**0.75**	0.54
		% of variance	67.0	13.5
Wet	**spruce**	**1**	**0.87**	0.37
		2	**0.87**	0.41
		3	**0.92**	0.27
		4	**0.89**	0.38
		5	**0.89**	0.35
	subalpine fir	**1**	0.20	**0.85**
		2	0.63	**0.65**
		3	**0.70**	0.58
		4	0.37	**0.68**
		5	**0.69**	0.59
		% of variance	76.6	7.5

Table 2.4. Summary statistics of the regionally- and species-specific chronologies. Chronologies were standardized using a cubic spline. Mean sens., Std. dev., and AC(1) are mean sensitivity, standard deviation and first order autocorrelation, respectively. Mean r_{bt} is the mean correlation between trees.

Variant	Species	N	Start	Mean sens.	Std. dev.	AC (1)	Mean r_{bt}
Dry (early)	**spruce**	72	1876	0.12	0.15	0.50	0.50
	subalpine fir	65	1873	0.12	0.15	0.58	0.37
Dry (late)	**spruce**	50	1788	0.14	0.19	0.54	0.41
	subalpine fir	47	1804	0.14	0.19	0.59	0.49
Mesic	**spruce**	44	1772	0.13	0.17	0.55	0.41
	subalpine fir	93	1774	0.19	0.25	0.59	0.44
Wet	**spruce**	95	1790	0.15	0.20	0.50	0.53
	subalpine fir	80	1828	0.12	0.15	0.47	0.36

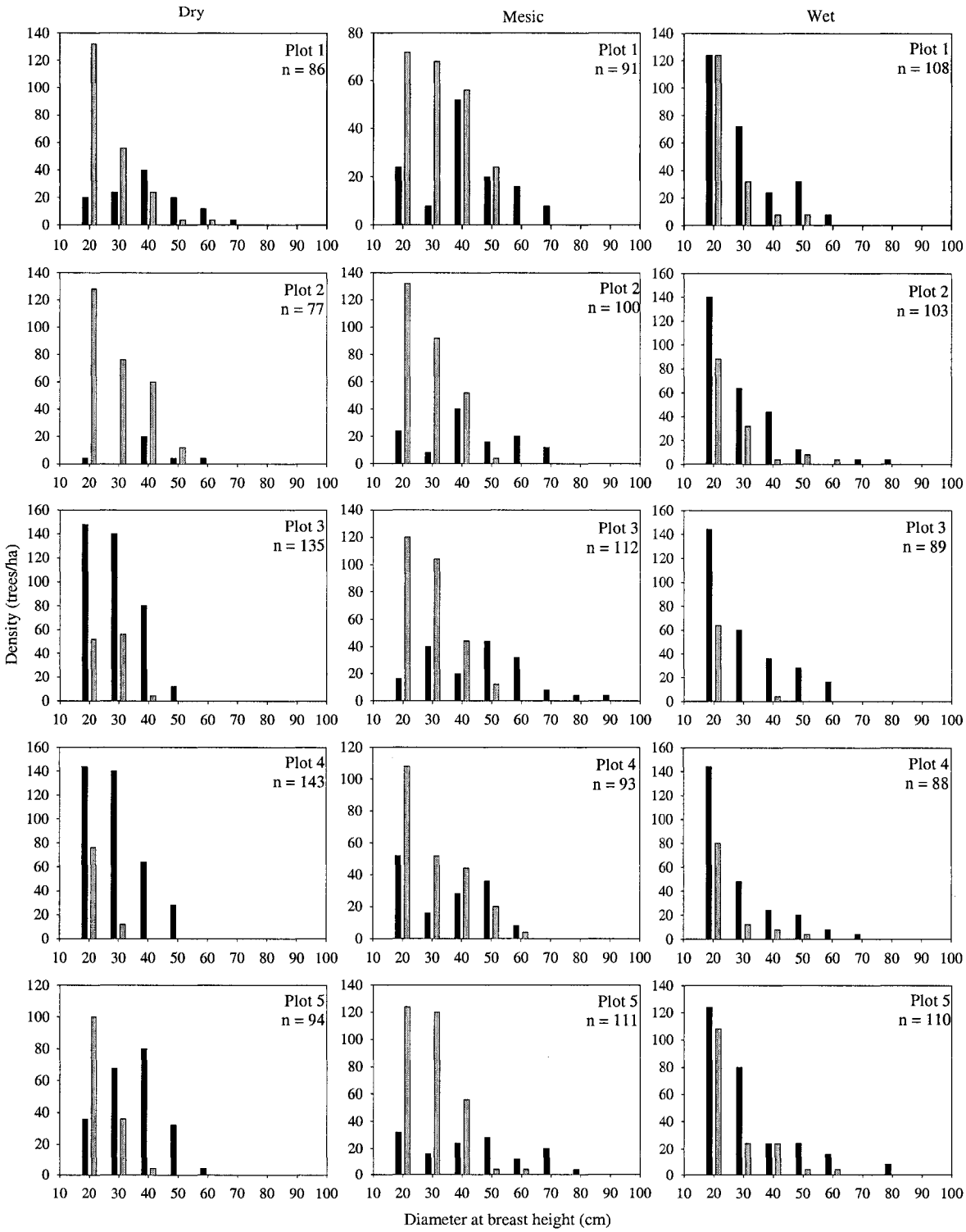

Figure 2.1. Diameter distributions of living spruce (black) and subalpine fir (grey) for the 15 study plots. Plots are grouped as dry (left), mesic (middle) and wet (right) variants. Midpoints of each diameter-class are indicated on the x-axis.

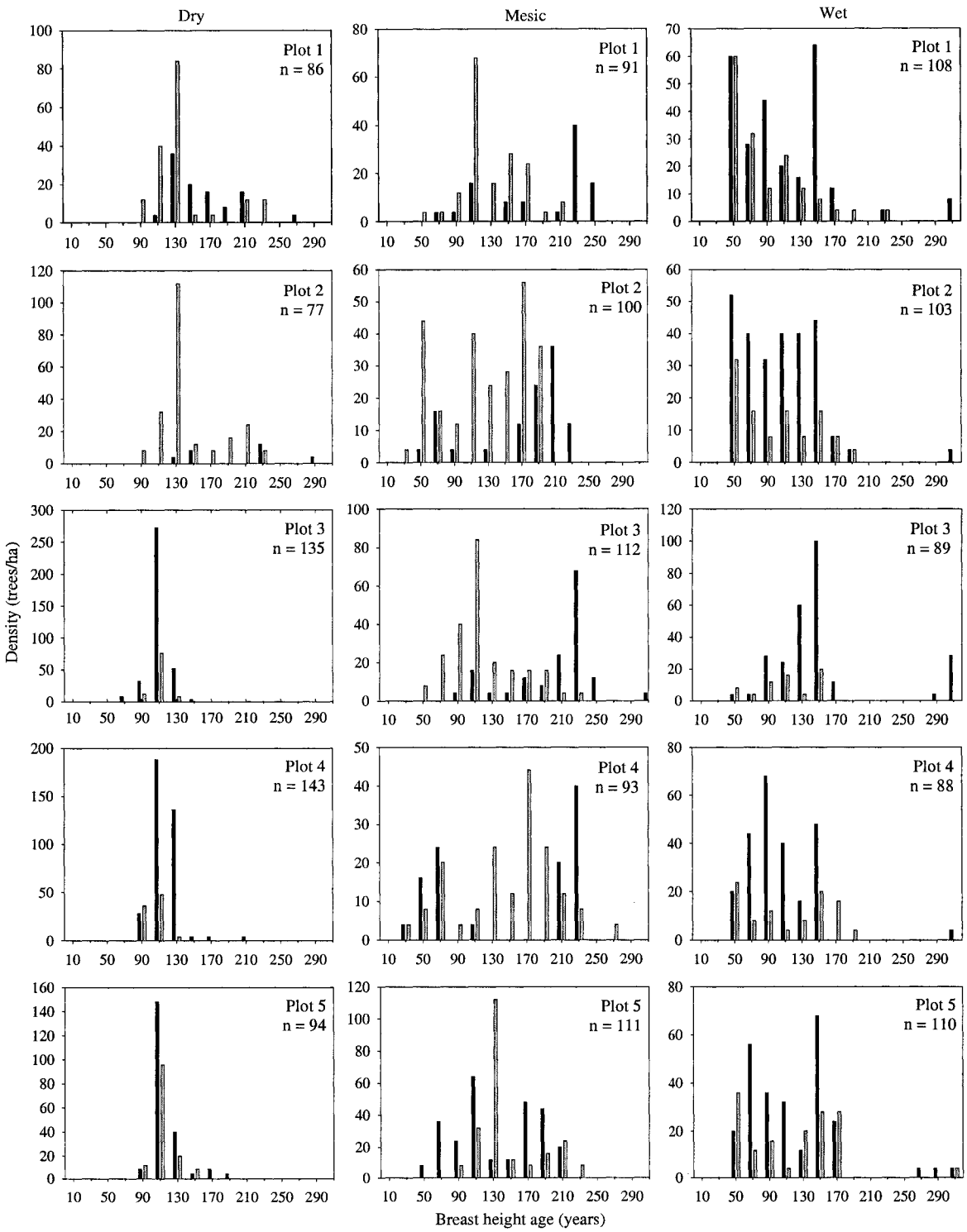

Figure 2.2. Distributions of breast height age of living spruce (black) and subalpine fir (grey) for the 15 study plots. Plots are grouped as dry (left), mesic (middle) and wet (right) variants. Midpoints of each age-class are indicated on the x-axis.

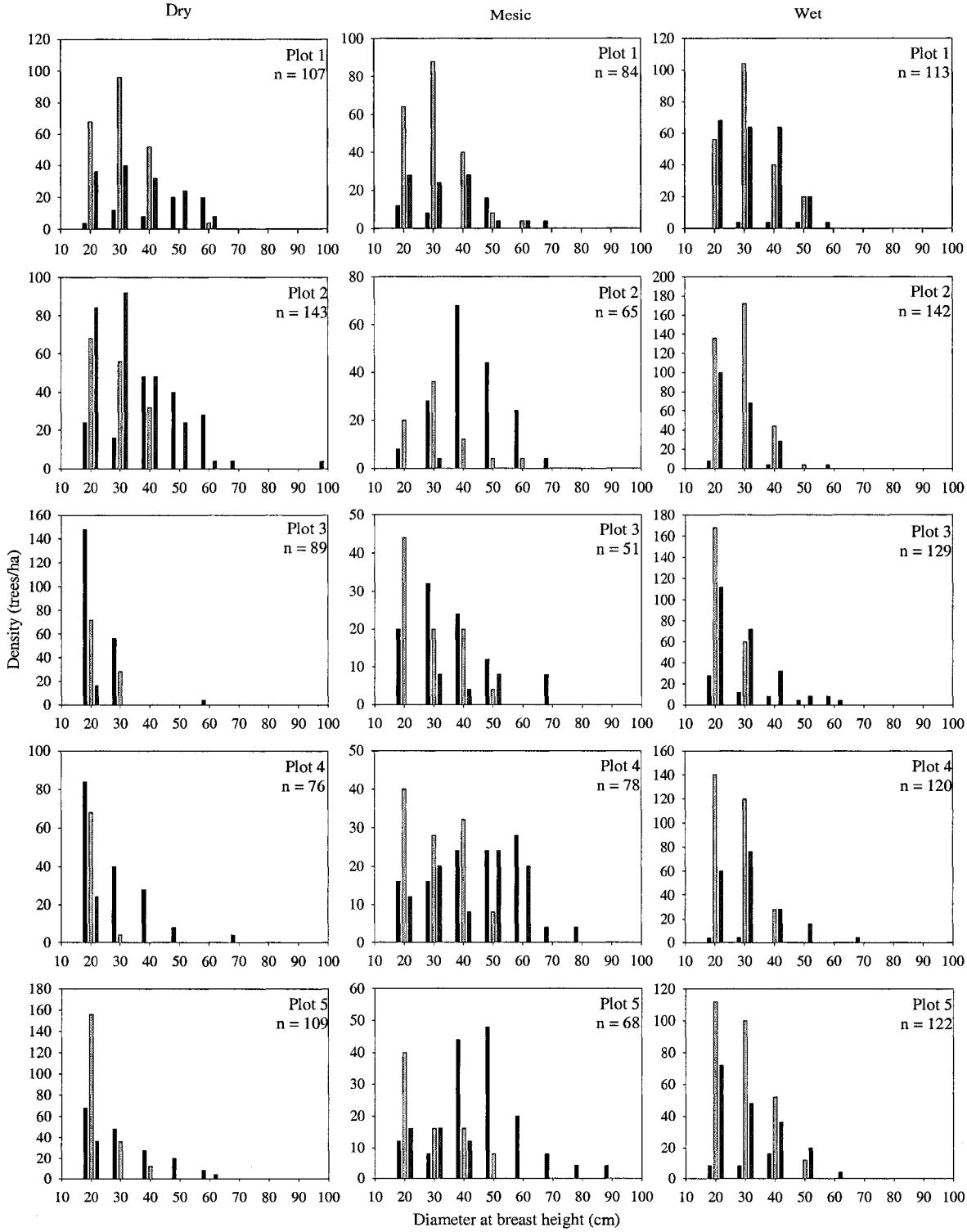

Figure 2.3. Diameter distributions of dead spruce (black), subalpine fir (grey) and unidentifiable species (dark grey) for the 15 study plots. Plots are grouped as dry (left), mesic (middle) and wet (right) variants. Midpoints of each diameter-class are indicated on the x-axis.

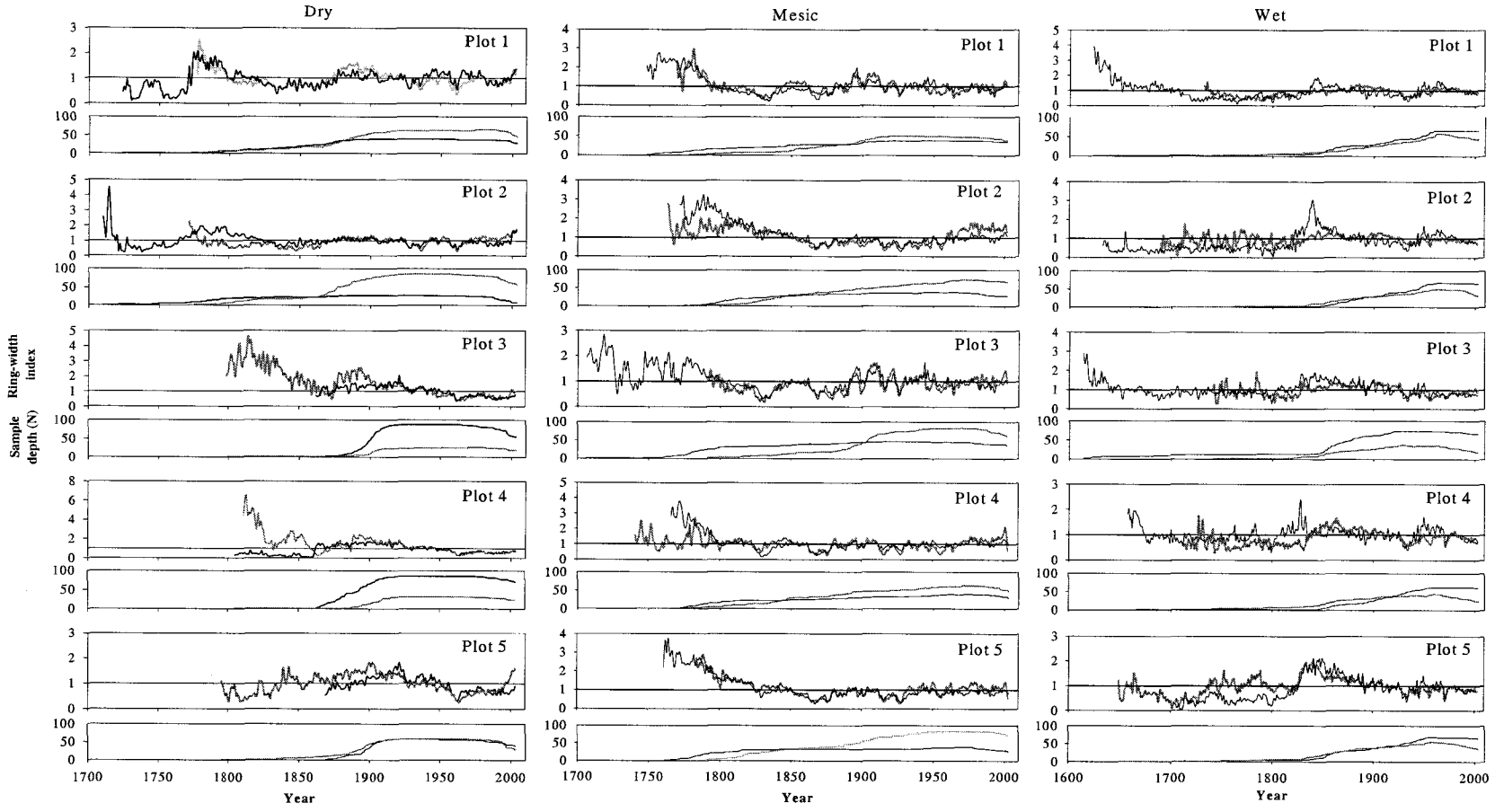

Figure 2.4. Species-specific, standard ring-width chronologies for the 15 study plots. Black and grey lines represent spruce and subalpine fir, respectively. Chronologies were standardized using a horizontal line. The sample depth curves represent the number of cores used to calculate the yearly ring-width indices.

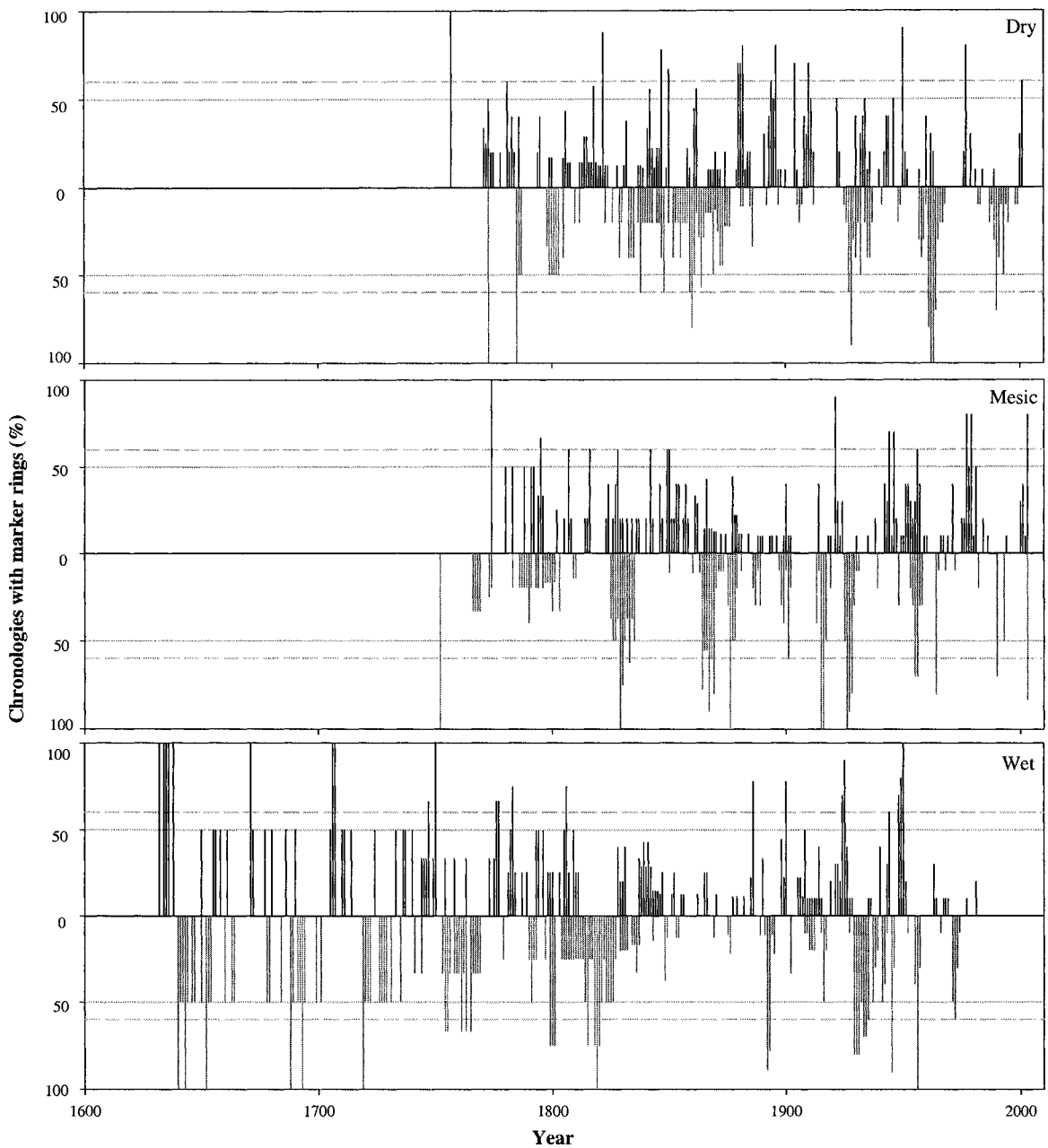

Figure 2.5. Percentage of cubic-spline chronologies showing marker rings in each year. Black and grey bars represent positive (wide) and negative (narrow) marker rings, respectively.

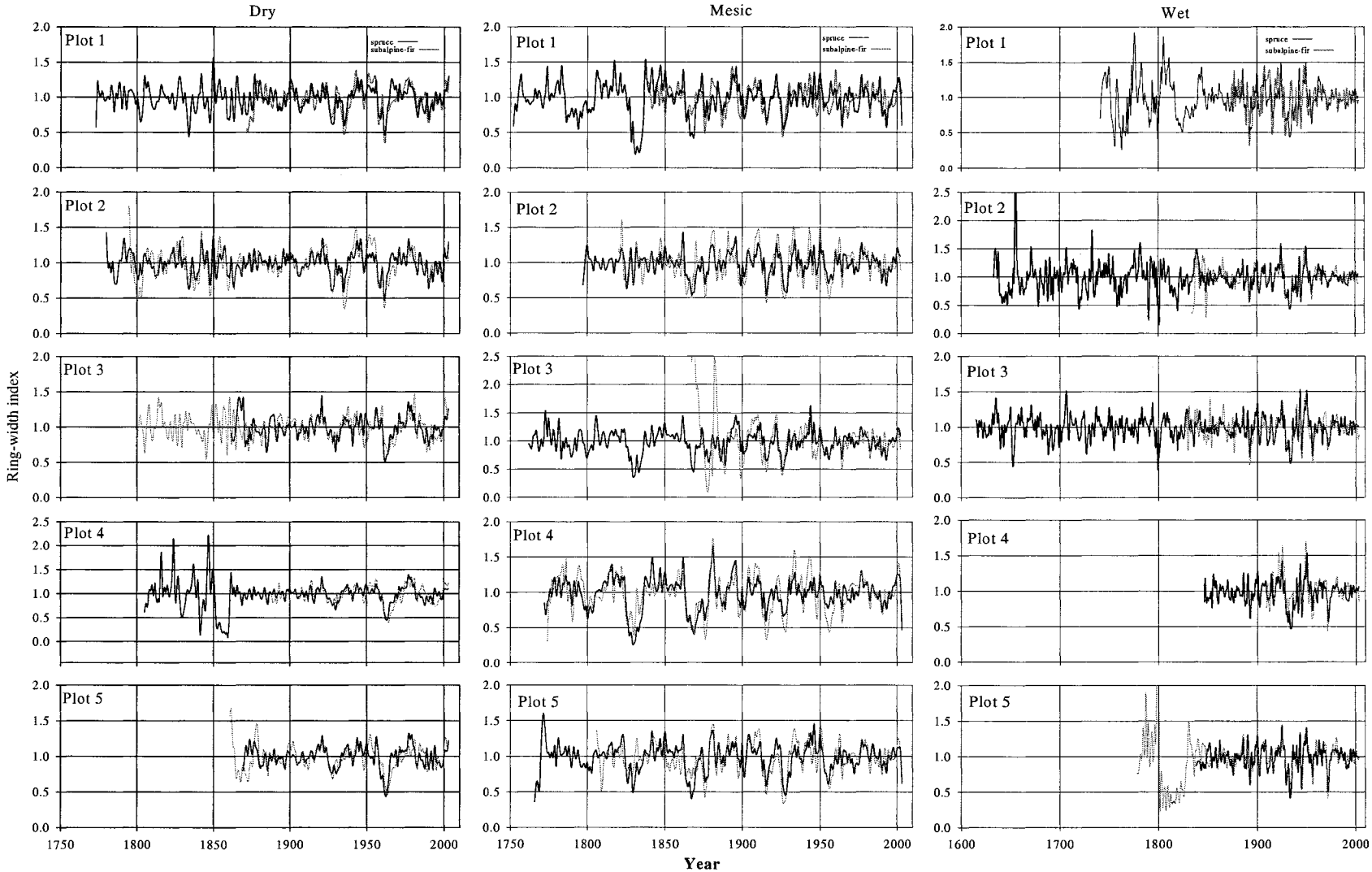

Figure 2.6. Species-specific, standard ring-width chronologies for the 15 study plots. Black and grey lines represent spruce and subalpine fir, respectively. Chronologies were standardized using a cubic-spline.

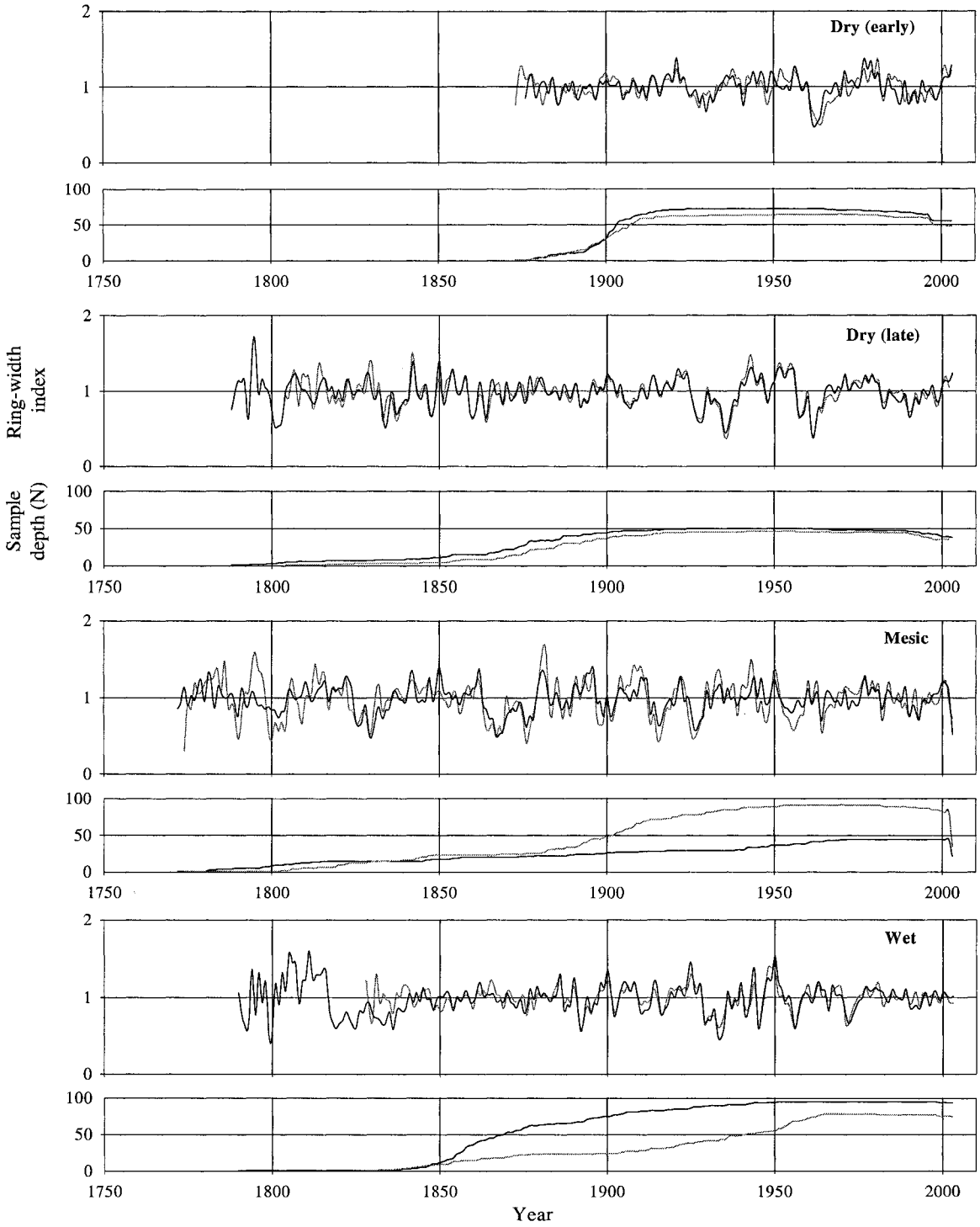

Figure 2.7. Regional- and species-specific chronologies. Black and grey lines represent spruce and subalpine fir, respectively. Ring width series were standardized using a cubic spline of 50% frequency response of 50 years. The sample depth curves represent the number of cores used to calculate the yearly ring-width indices.

CHAPTER 3 - USING TREE RING GROWTH RATE CRITERIA TO ASSIGN DATES OF CANOPY DISTURBANCE IN MATURE SPRUCE-SUBALPINE FIR FORESTS OF CENTRAL BRITISH COLUMBIA: DENDROECOLOGICAL CONSIDERATIONS II

Abstract

Year of gap-origin and/or release from suppression, corresponding to developmental canopy openings caused by the death of single and multiple trees, can be used to study disturbance regimes by estimating disturbance frequency and intensity. This chapter summarizes the development of two radial-growth-rate criteria used to assign dates of canopy disturbance in mature spruce-subalpine fir forests of central British Columbia. Three ecological variants were selected: dry sub-boreal, mesic sub-boreal and wet subalpine. Within each variant, five 0.25-ha plots were located in mature spruce-subalpine fir stands (n = 15). Within each plot, two sampling methods were used. First, each plot was subdivided into 16 evenly spaced grid points. At each point cores where extracted from the closest gap-maker/gap-filler pair. Year of death in each gap-maker was estimated by crossdating. If a pattern of release in the gap-filler was visually apparent ±10 years of the gap-maker year of death then the gap-filler was classified as a release tree, and percent change in radial growth was calculated (n = 117). Second, from the 16 grid points, four were randomly selected and 3.99m radius subplots were established for a total of 20 plots within each variant. In each subplot, saplings (height >1.3 m and dbh <15 cm) were classed as either shaded or receiving direct sunlight in a canopy gap. Disc or core samples were collected from each sapling 30 cm above the point of germination. Early growth rates were calculated as the average width of five consecutive annual rings, beginning at the first annual ring two cm from the pith (n =

422). From these data growth rate criteria were developed. The criteria are as follows: (1) for spruce and subalpine fir, gap-origin criteria for the dry, mesic and wet variants were set at 1.05, 0.9 and 0.8 mm/year, respectively, and (2) for spruce and subalpine fir across all ecological variants the release criterion was a 60 % increase in radial growth rates, when comparing adjacent 15-year periods.

Introduction[1]

Several dendroecological methods have been developed to reconstruct disturbance histories within forests of complex age structure. These methods can be classified as direct or indirect. Direct methods involve the cross-dating of dead samples to determine the year of death and require that samples have intact sapwood. Indirect methods involve: (1) predictive models that estimate the year of death; or (2) ring-width growth rate criteria that identifies the date a living tree had released from suppression, or the date a tree had established in a canopy opening caused by the death of a neighbouring tree.

The direct method of cross-dating involves the statistical comparison of overlapping segments of dead ring-width series against live series (Holmes 1983, Grissino-Mayer *et al.* 1994). Daniels *et al.* (1997) found that cross-dating could be used to date tree rings and assign the year of death for *Thuja plicata* Donn *ex* D. Don logs and snags. Storaunet and Rolstad (2002) found that *Picea abies* (L.) Karst logs, with intact sapwood on at least one portion of the length or circumference, could be used to estimate the number of years since death by cross-dating. As time passes, however, the ability to successfully cross-date samples to estimate the year of death diminishes. A sample can still be precisely dated, but the accuracy of that date for estimating year of death decreases as the log decays and the outer rings are lost.

The first group of indirect methods – using predictive models to estimate time since death – is based on the reality that snags and logs inevitably decay over time. Storaunet (2004), using *Picea abies* snags, developed a time-since-death model that predicted year of

[1] A version of this document will be submitted for publication under multiple authors. All data used in this study were collected by R. D. Thompson and a number of field and lab assistants. In this thesis I use 'we' and 'our' to reflect the involvement of others in various aspects of this work.

death based on levels of snag decomposition. Newbery *et al.* (2004), using *Picea engelmannii* × *glauca* Voss × Parry and *Abies lasiocarpa* (Hook.) Nutt. snags and logs from 70-year-old permanent sample plots, developed time-since-death models based on species, position (i.e., standing and down) and levels of decomposition. Due to the 70-year limitation of the data, as well as the increasing error variance in the decomposition variables, Newbery *et al.* (2004) suggested that the models be restricted to 70 years before present, making it difficult to reconstruct long disturbance histories.

The second group of indirect methods – involving the development of growth rate criteria – uses absolute growth and relative changes in growth in live canopy trees to date canopy disturbance. Lorimer *et al.* (1988) and Lorimer and Frelich (1989) developed two indirect methods to date canopy disturbance. First, they used rapid early growth-rates to indicate origin of a tree in a gap. Gap-origin criteria are used to estimate the probability of gap-origin for current canopy trees, and are developed by integrating the early growth rates of currently suppressed and open grown saplings (Lorimer *et al.* 1988, Lorimer and Frelich 1989). Second, the authors used abrupt and sustained increases in growth to indicate release from suppression as a response to the death of a dominant neighbouring tree. Ring-width series taken from recent gap-maker trees can grade between patterns of slow decline resulting from root disease (Lewis 1997) to a more sudden cessation resulting from windthrow, bole breakage or bark beetle attack. In the former case, gap-filling trees may show complex or ambiguous growth patterns (Lorimer and Frelich 1989). In the latter case, abrupt and sustained increases in radial growth within the ring-width series of gap-filling trees are expected and indicate that a tree has released from suppression due to the mortality of a dominant neighbouring tree (Lorimer and Frelich 1989, Newbery 2001). To identify disturbance-caused release from suppression, and to integrate these events into release

criteria, mortality dates of recent gap-maker trees can be estimated by cross-dating and compared with ring-width series from gap-filling trees (Newbery 2001).

Daniels *et al.* (1997) point out a number of differences that can occur between direct and indirect methods. First, trees do not necessarily die and fall immediately. Whether a tree remains standing or falls down after it dies, and how long it has been in each position, will influence its exposure to physical weathering and susceptibility to decay organisms (Newbery *et al.* 2004). Therefore, the decay rates of snags and downed trees will differ. Second, the outermost rings naturally erode following death, or ring formation can often cease prior to tree death, making it impossible to date mortality accurately. Finally, there can be lengthy delays in tree establishment or release after any disturbance event (Cherubini *et al.* 1996, Mast and Veblen 1994). Considering the above phenomena, it is impossible for one method alone to capture all disturbance events. Ideally, a collection of direct and indirect methods should be used to describe disturbance processes over lengthy temporal scales.

The objectives of the following study were to: (1) develop and calibrate a suite of dendroecological tools to quantify the effects of fine-scale disturbance events (i.e., single and multiple tree mortalities) across three distinct sub-boreal and subalpine ecosystems of central British Columbia; and (2) to test for differences between spruce and subalpine-fir, two common coniferous species found across central British Columbia.

Materials and Methods

Field sampling

We selected three biogeoclimatic variants to represent the climatic gradient that spans the dry-warm interior plateau to the wet-cold foothills of the Canadian Rockies (Chapter 1, Figure 1.1). The Stuart Dry Warm Sub-Boreal Spruce (SBSdw3), Willow Wet Cool Sub-

Boreal Spruce (SBSwk1) and Misinchinka Wet Cool Engelmann Spruce-Subalpine Fir (ESSFwk2) biogeoclimatic variants are located in two of the most common biogeoclimatic zones located in central British Columbia. The SBSdw3, SBSwk1 and ESSFwk2 biogeoclimatic variants will be referred to as the dry, mesic and wet variants, respectively.

Within each variant, we selected five forest stands. Stands were selected using several criteria. First, forest stands were beyond the stem exclusion stage as defined by Oliver and Larson (1996). This criterion was used to select stands in which trees were establishing in the understorey and, in the absence of stand-replacing disturbances, were advancing toward the true old-growth stage of development (Oliver and Larson 1996). Second, forest soils had intermediate soil moisture (mesic) and nutrient (mesotrophic) regimes (Meidinger and Pojar 1991). This criterion was intended to minimize variation in tree species growth characteristics and disturbance processes as a result of highly divergent edaphic influences of soil moisture and nutrients. Third, forest stands had a mixture of spruce and subalpine fir as the dominant component of the canopy, with basal area >80 %, for all trees over 15 cm diameter at breast height (dbh, measured 1.3 m above the ground). A common tree composition and density minimized variation in stand susceptibility to disturbance. Finally, forest stands had no evidence of industrial forest activities. This final criterion ensured that stand dynamics resulted from natural disturbances, which may include past traditional uses and practices of First Nations. Consequently, stands are not representative of the average of the biogeoclimatic variant, but rather, they are typical of stands satisfying the criteria within each variant.

Within each stand, one 0.25-ha (50-m × 50-m) plot was randomly placed, for a total of 15 plots. All living trees equal to or greater than 15 cm diameter at breast height (dbh, 1.3 m) were numbered, species tallied and dbh measured.

Dendroecological materials and procedures

From each 0.25-ha plot, increment cores were taken at breast height from each live tree. Cores were taken at breast height because they tend to have less stem decay enabling maximum ring-width series. Cores were prepared following the standard dendrochronology techniques of Stokes and Smiley (1968). Individual ring-width series were measured to the nearest 0.01 mm using WinDENDRO (Regent Instruments Inc. 2000). For all core samples that had periods of extremely small ring-widths (≤0.5 mm) the series were measured to the nearest 0.001 mm using the Velmex "TA" System (Velmex, Inc. 1992) in conjunction with MeasureJ2X (2004). The computer program COFECHA (Holmes 1983) was used to assist in the detection of measurement and cross-dating errors. Once the ring-width series were dated, the growth rate criteria outlined in the following sections were applied to each ring-width series. Decadal frequency distributions of gap-origin and release from suppression were plotted for spruce and subalpine fir separately for each plot and used to visually assess for possible sources of error in the application of the criteria.

Early growth rates and gap-origin criteria

Each plot was subdivided into 16 evenly spaced grid points using a 10-m × 10-m grid, excluding all boundary points. From the 16 grid points, four were randomly selected. At each selected grid point a 3.99-m ($1/200^{th}$ ha) radius subplot was established for a total of 20 plots within each variant. Within each subplot, saplings (height >1.3 m and dbh <15 cm) were classed as either shaded (i.e., suppressed by canopy trees) or receiving direct sunlight in a gap (i.e., gap-origin). Gaps were defined as openings in the canopy that have resulted from the death of one or more trees, where evidence of the dead tree still exists, and in which

regeneration is less than half the average height of the living canopy trees at the canopy margin (Worrall and Harrington 1988). Discs were taken for smaller saplings 30 cm above the point of germination. For large saplings cores were taken 30 cm above the point of germination. The early growth rate was calculated for each sapling as the average width of five consecutive annual rings beginning at the first annual ring two cm from the pith (Lorimer *et al.* 1988). For core samples that did not include the pith, the distance to the pith was estimated using the geometry of an arc defined by the inner incomplete ring. If the estimated distance was < two cm, the sample was kept, and the early growth rate was calculated as the first five rings. Early growth rates (mm/year) of current saplings in the four cm dbh class were measured as the average width of the last five rings (Lorimer *et al.* 1988). We assumed that all sapling growth rates were comparable because the measured rings all came from a narrow size-class (i.e., ≈2-6 cm). Saplings with damaged or bowed stems were excluded from analyses.

Difference in the early growth rates between sapling class, species and variant were analyzed by nested ANOVA, with species nested within variant (Zar 1996, SPSS Inc. 1999). Explanatory variables in the nested ANOVA were treated as random effects. The number of criteria used to define "gap-origin" was based on differences in the explanatory variables. The frequency distributions of gap-origin and suppressed sapling early growth rates were plotted using 0.5 mm/year growth rate classes.

The probability that a canopy tree was growing in a gap, when in the four cm dbh class, given an observed early growth rate, is dependent on the degree of overlap in the growth rate frequency distributions of the suppressed vs. gap-origin saplings. Likewise, the probability that a tree was initially suppressed is determined partly by the percentage of gap saplings exceeding a stated growth threshold, as well as by the relative abundance of the two

sapling types and the differential probability of both surviving to maturity. Equation [1] below states that the probability that a sample tree was growing in a gap, when in the four cm dbh class, given an observed growth rate, X, equal to or greater than a specified threshold growth rate, x, is numerically equal to the ratio of the proportion of gap saplings exceeding growth rate x to the proportion of both suppressed and gap saplings exceeding the threshold (Lorimer and Frelich 1989):

$$[1] \qquad P(gap|X \geq x) = \frac{G_{xi} \bullet Q'_g}{(S_{xi}Q'_s) + (G_{xi}Q'_g)}$$

where:

G_{xi} = proportion of gap saplings in size class i exceeding growth rate x;

S_{xi} = proportion of suppressed (understory) saplings of size class i exceeding growth rate x;

Q'g = overall proportion of trees in the stand that were growing in gaps when four cm dbh; and

Q's = overall proportion of trees in the stand that were suppressed when four cm dbh.

S_{xi} and G_{xi} are calculated directly from the contemporary sapling growth rate distributions. Q's and Q'g are historical estimates obtained from radial patterns and growth rates of mature trees (Lorimer *et al.* 1988). The formula is then used in an iterative process until $P_{xi} = 95\%$.

Percent change in radial growth and release criteria

Within each plot, from the 16 grid points defined in the previous section, one core or disc was taken from the closest gap-maker. These ring-width series were cross-dated against species- and plot-specific master chronologies, developed in Chapter 2, using the computer

program COFECHA (Holmes 1983) to estimate year of death. The year of death was then compared to possible years of release identified from the ring-width series of the two closest potential gap-filler trees taken from intermediate and suppressed crown classes (Newbery 2001). If the year of release occurred within 10 years of the year of death then the tree was classified as a gap-filler tree and the percent change in radial growth was calculated from the ring-width series as:

$$[2] \qquad \%CRG = \left(\frac{GRA_m - GRB_n}{GRB_n} \right) * 100$$

where:

%CRG = percent change in radial growth;

GRB_n = the average growth increment based on n years of growth before the date of mortality in the gap forming tree; and

GRA_m = the average growth increment based on m years of growth after the date of mortality in the gap forming tree.

The values of n and m were selected using empirical data resulting from the species/regionally-specific cubic-spline chronologies developed in Chapter 2 and the findings of Lorimer *et al.* (1988) and Lorimer and Frelich (1989). The value n, the number of years prior to the date of mortality, was used to avoid classifying recovery from extended periods of climate-related below average growth as gap-related release from suppression. The 95th-percentile, based on the frequency distribution of below average growth (i.e., ring-width indices less than zero for ≥ three years), was used as a first estimate of n. The value of m, the number of years after the date of mortality, was used to avoid classifying extended periods of climate-related above average growth as gap-related release from suppression. The 95th-

percentile, based on the frequency distribution of above average growth (i.e., ring-width indices greater than zero for ≥ three years), was used as a first estimate of m. In addition, existing canopy trees can fill in gaps through lateral expansion given relatively high initial stem densities (Lorimer and Frelich 1989). Therefore, a highly conservative value of m was required to eliminate the classification of responses to crown thinning (i.e., trees in the canopy responding to the death of other trees in the canopy) as release, despite a possibility of missing true release events.

To assess the need for multiple release criteria, differences in the percent change in radial growth by ecological variant and by species were analyzed using nested ANOVA, with species nested within variant (Zar 1996, SPSS Inc. 1999). Explanatory variables in the nested ANOVA were treated as random effects. The frequency distributions of percent change in radial growth were plotted using 50 % classes. A relatively high percent release value was chosen (25^{th}-percentile) because adjacent mortality usually causes weaker growth increases than overhead releases (Lorimer and Frelich 1989, Newbery 2001).

Results

Early growth rates and gap-origin criteria

Early growth rates of saplings were positively skewed (Figure 3.1, n = 422). To meet the ANOVA assumptions of normality and homogeneity of variance, the data were transformed using the Box-Cox transformation (Sokal and Rohlf 1995). Although the distributions of early growth rates overlapped between saplings that were initially suppressed and saplings that originated in gaps (Figure 3.1), the nested ANOVA detected a significant difference between the two sapling classes (Table 3.1). Although there was no significant difference between ecological variant at conventional alpha levels, the results suggest that a

proportion of the variation in early growths rates can be explained by ecological variant (Table 3.1). No significant difference between the early growth rates of spruce and subalpine fir was found (Table 3.1). Based on these results, criteria were developed for each variant to identify spruce and subalpine fir canopy samples that showed rapid early growth rates (Figure 3.1). Using the formula to determine rapid early growth rates with 95 % confidence levels, the threshold values for the dry, mesic and wet variants were set at 1.05, 0.9 and 0.8 mm/year, respectively.

Based on the gap-origin criteria, within the dry variant, plots 1 and 2 show a period of establishment after 1870, and plots 3, 4 and 5 show a period of establishment after 1880 (Figure 3.2). Within the mesic variant, the gap-origin frequencies show a wide range in the number of trees establishing in each decade and minor synchronicity in establishment dates across all plots (Figure 3.2). Within the wettest sites, the gap-origin frequencies also show a wide range in the number of trees establishing in canopy openings during each decade (Figure 3.2). Furthermore, two common periods of establishment are evident after 1850 and 1930 (Figure 3.2).

Percent change in radial growth and release criteria

Based on the species/regionally-specific chronologies developed in Chapter 2, the mean duration of below average growth was four years, ranging from 3-16 years, and the 95th-percentile was 12 years. A conservative "15-year growth increment" before the date of mortality in the gap forming tree (GRA_m) was selected. The mean duration of above average growth was five years, ranging from 3-13 years, and the 95th-percentile was 10 years. A conservative "15-year growth increment" after the date of mortality in the gap forming tree (GRB_n) was selected.

The distribution of percent change in radial growth was positively skewed (Figure 3.3). To meet the ANOVA assumptions of normality and homogeneity of variance, the data were transformed using the Box-Cox transformation (Sokal and Rohlf 1995). The nested ANOVA detected no significant differences in the percent change in radial growth values between ecological variant or between spruce and species nested within ecological variant (Table 3.2). Based on these results, one criterion for release was developed based on the pooled data (Figure 3.3, n = 121). Fifty percent of the observations for percent change in radial growth fell between 60 and 230 % with the median being 116 %. Based on the 25th-percentile, a 60 % increase in radial growth was chosen to identify release from suppression caused by canopy disturbance.

Based on the release criterion, within the driest sites, plots 1 and 2 show an increased number of release events during the 1940s, and all plots show an increase in the number of release events during the 1960s (Figure 3.4). Within the mesic sites, three common periods of release occurred during the 1870s, 1930s and 1960s (Figure 3.4). Within the wettest sites, one common period of release occurred during the 1930s into the 1940s (Figure 3.4)

Discussion

The results of this study clearly demonstrate that radial-growth-rate criteria can be used to date fine-scale (i.e., tree-level) disturbance. Furthermore, in comparison with previous work, early growth rates and release from suppression can show a wide range in variation by species or by region of study, and therefore suggests that radial-growth-rate criteria must be calibrated to account for variation within the specific ecosystems studied.

In regard to gap-origin criterion, the results of this study suggest that grouping species into one gap-origin criteria for each ecological variant is conservative and parsimonious.

Using formula [1] to determine the gap-origin criteria, with 95% confidence levels, the threshold values for the dry, mesic and wet variants were set at 1.05, 0.9 and 0.8 mm/year, respectively. Antos and Parish (2002a) and Parish *et al.* (1999), using early growth rates to identify gap-origin, did not separate species and defined initial rapid growth as ring-widths ≥1.0 mm/year within the first 25 years and sustained for 10 years thereafter for *Picea engelmannii* Parry ex Engelm. and *Abies lasiocarpa* within the subalpine forests of southern British Columbia. In contrast, Newbery (2001) adapted the methods of Lorimer *et al.* (1988) and Lorimer and Frelich (1989) for *Picea glauca* × *engelmannii* and *Abies lasiocarpa* in the sub-boreal forests of central British Columbia and found significant differences in the early growth rates of the two species, and set the gap-origin criteria at ≥1.7 mm/year and ≥1.5 mm/year, respectively. Although his results suggested a statistically significant difference between the early growth rates of spruce and subalpine fir, the difference was not large, suggesting that the early growth rates are generally the same when establishing in canopy gaps.

Wright *et al.* (1998) showed that in continental subalpine environments the radial growth of spruce and subalpine fir converged at high light levels. Wright *et al.* (1998) also showed that radial growth rates of subalpine fir and spruce were similar at light levels <20 % full sun. Furthermore, Coates (2000) found very little difference between spruce and subalpine fir in mean seedling diameter five years after planting within undisturbed forest, and extending up to medium gap sizes (300 to 1000 m^2). Within our present study, the canopy openings are caused by the death of single and multiple trees. It is reasonable to assume that the spruce and subalpine fir saplings we sampled come from canopy openings well within the range investigated by Coates (2000). Grouping species into one gap-origin

criteria for each ecological variant is practical for the ecological variants selected within our study.

In regard to release criteria, when comparing the results of our study with previous silvicultural and historical reconstructions of disturbance, pooling data to develop one release criterion for all species across all ecological variants is appropriate. Based on these pooled data, a release event was defined as a ≥60 % increase in mean radial growth, when adjacent groups of 15 years are compared.

Most silvicultural studies show that typical release from suppression falls within a range of 40 to 100 %. The release criterion selected for this study is well within this range. The response of individual hardwoods to heavy commercial type thinning (including *Acer rubrum* L., *Acer saccharum* Marsh., *Prunus serotina* Ehrh., *Liriodendron tulipifera* L., and *Quercus rubra* L.) have indicated growth releases between 70 and 90 % (Stone 1977, Ellis 1979, Erdmann *et al.* 1985, Lamson *et al.* 1990, Smith and Miller 1991, in Singer and Lorimer 1997). Ellis (1979) reported that *A. saccharum* in an 85-year-old stand given full crown release had a mean diameter growth rate increase of 94 %. Jones and Thomas (2004) found that *A. saccharum*, within the 10 to 25 cm diameter class, averaged a 50 % increase in diameter growth four years after harvest. Singer and Lorimer (1997) found that basal area growth rates in mature northern hardwoods can be increased on average by 70 to 100 % using heavy commercial type thinning.

Similar results have been found in coniferous forests dominated by *Picea* spp. and/or *Abies* spp. Balvinder *et al.* (2001), for example, found an average diameter increase of 37 % in response to glyphosate treatments in a 16-year-old *Picea glauca* (Moench) Voss plantation. Biring *et al.* (1999) reported an 85 % increase in growth in *Picea glauca* and *Abies balsamea* (L.) Miller over 12 years following glyphosate treatment. Sutton (1995)

found a 50 to 100 % increase in diameter growth in a 30-year-old *Picea glauca* stand following fertilization, weed control and irrigation.

Historically, the selected release criteria used to quantify fine-scale disturbance frequencies and intensities fall inline with the range of release responses reported within the silvicultural studies. Cherubini *et al.* (1996) defined release from suppression as a sudden increase of at least 40 % over the previous four years. Lorimer and Frelich (1989) and Abrams and Orwig (1996) defined a major release as an average growth increase ≥100 %, and a moderate release as an average growth increase between 50 to 100 %. Nowacki and Abrams (1997) used a 25 % increase in radial growth as a cut-off for the detection of minor releases, such as those created by single tree removal. Parish *et al.* (1999) defined a release as a 100 % increase in ring-width, sustained for at least 10 years. Veblen (1986) used a 150 % increase criterion for *Picea glauca* × *engelmannii* and *Abies lasiocarpa,* but required releases to be sustained only five years. For the same species, Newbery (2001) used a 65 % increase in growth based on a 15-year slow growth-rate criteria before release followed by a 15-year sustained release criteria. These release criteria are intended to be strict enough to screen out most cases of climatic, thinning, and side-lighting responses, but not so strict that valid releases would often be excluded and disturbance frequencies and intensities underestimated (Lorimer and Frelich 1989). Based on the above evidence regarding release caused by silvicultural research treatments and release criteria used in previous studies, a 60 % growth increase (which corresponds to the 25th-percentile in the percent change in radial growth change data distribution) based on a "15-year sustained release criteria" and a "15-year slow growth before release criteria" is reasonable and conservative.

Although the gap-origin and release criteria developed within this study are highly conservative, Chapter 2 demonstrates that inferred climate events can result in growth

patterns that are similar to those caused by fine-scale disturbance. Together with the results of this study, this is clearly the case in a number of the plots (Figure 3.4). Within the central interior of British Columbia the mean durations of growth decrease and increase were four and five years. The maximum growth decrease and increase, however, were 16 and 13 years, respectively. Extended periods of growth decrease followed by growth increase have created pseudo-release patterns. This is visible as a majority of trees showing release from suppression in one time period across all plots. Based on an assessment of both release frequencies (Figure 3.4) and the species/regionally-specific cubic-spline chronologies developed in Chapter 2 (Figures 2.2 and 2.4), we can conclude that these events are climate driven, and not due to some intermediate- or coarse-scale disturbance event. For example, during the 1960s within the driest sites, one such climate event occurred and is of concern regarding future estimation of fine-scale disturbance frequencies. A comparison of the dry variant chronologies of Chapter 2 (Figures 2.2 and 2.4) suggests that the pattern is likely linked to climate because no abrupt and sustained release patterns occurred during the same decade in any of the SBSdw3 chronologies developed using horizontal-line standardization.

Lorimer and Frelich (1989) found that the identification of canopy disturbance, based on rapid early growth and release from suppression are accurate because the levels of uncertainty or ambiguity associated with these patterns are low. The results of this study clearly demonstrate that when these methods are applied to data sets taken from mature, spruce-subalpine fir dominated sub-boreal and subalpine forest types, the levels of uncertainty and ambiguity associated with growth responses to developmental canopy gaps can be minimized, but not removed completely. Multiple dendroecological methods, in addition to the radial growth rate criteria developed within this study, are absolutely necessary to validate the identification of fine-scale disturbance.

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Table 3.1. Nested ANOVA results of early growth rates between sapling class, ecological variant and between species nested within ecological variant.

Source	SS	df	MS	F	p
Sapling class	73.981	1	73.981	220.839	<0.001
Variant	5.522	2	2.761	8.242	0.058
Species (Variant)	1.006	3	0.335	1.530	0.206
Error	90.745	415	0.219		

Table 3.2. Nested ANOVA results of percent change in radial growth values between ecological variant and between species nested within ecological variant.

Source	SS	df	MS	F	p
Variant	33.939	2	16.970	1.298	0.393
Species (Variant)	39.221	3	13.074	0.837	0.476
Error	1796.902	115	15.625		

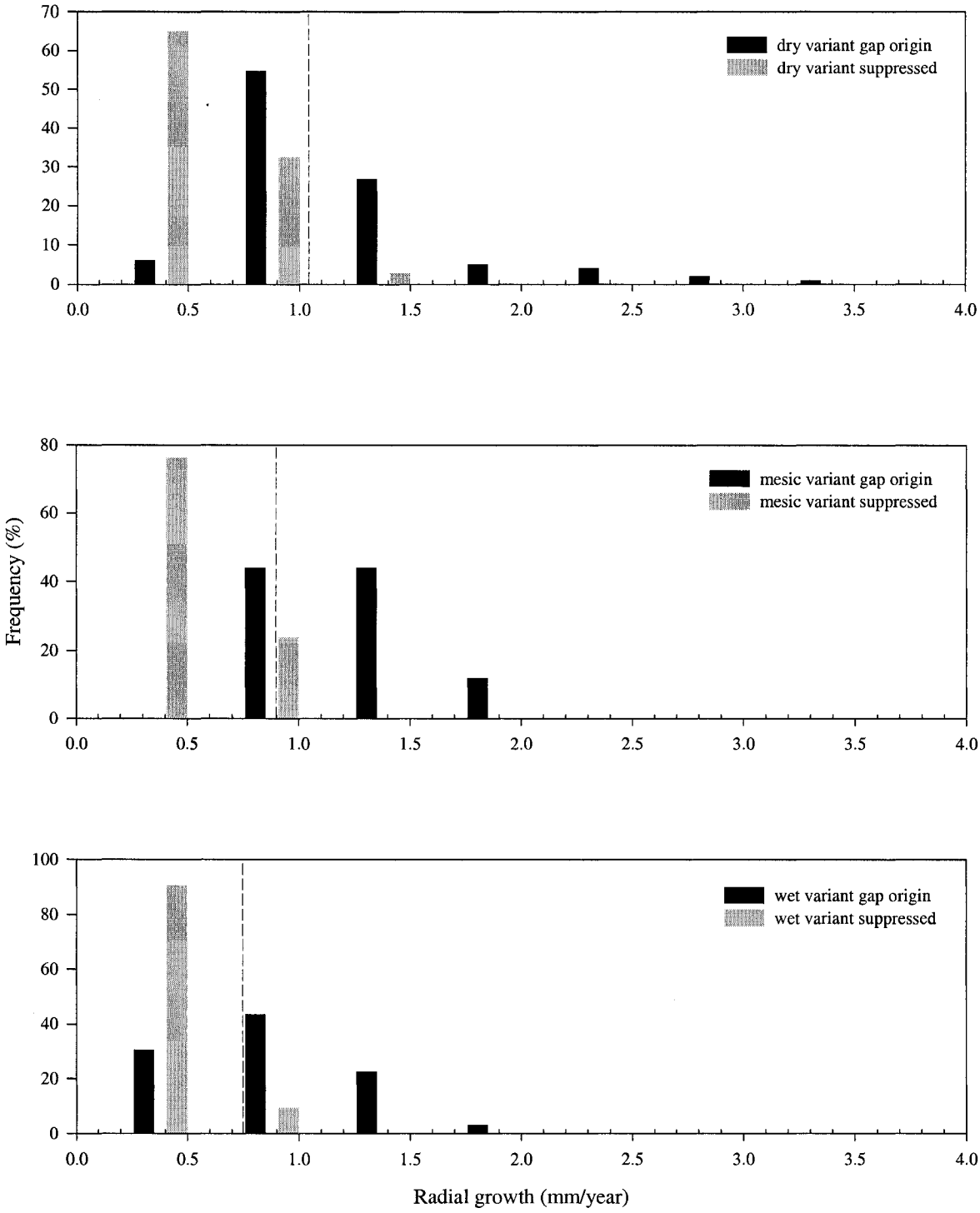

Figure 3.1. Frequency distributions of radial growth rates for gap-origin (black) and suppressed (grey) saplings, pooled by species. The dashed lines indicate the early growth rate (EGR) criteria for each ecological variant. Sample sizes for the dry, mesic and wet variants are 171, 71 and 180, respectively.

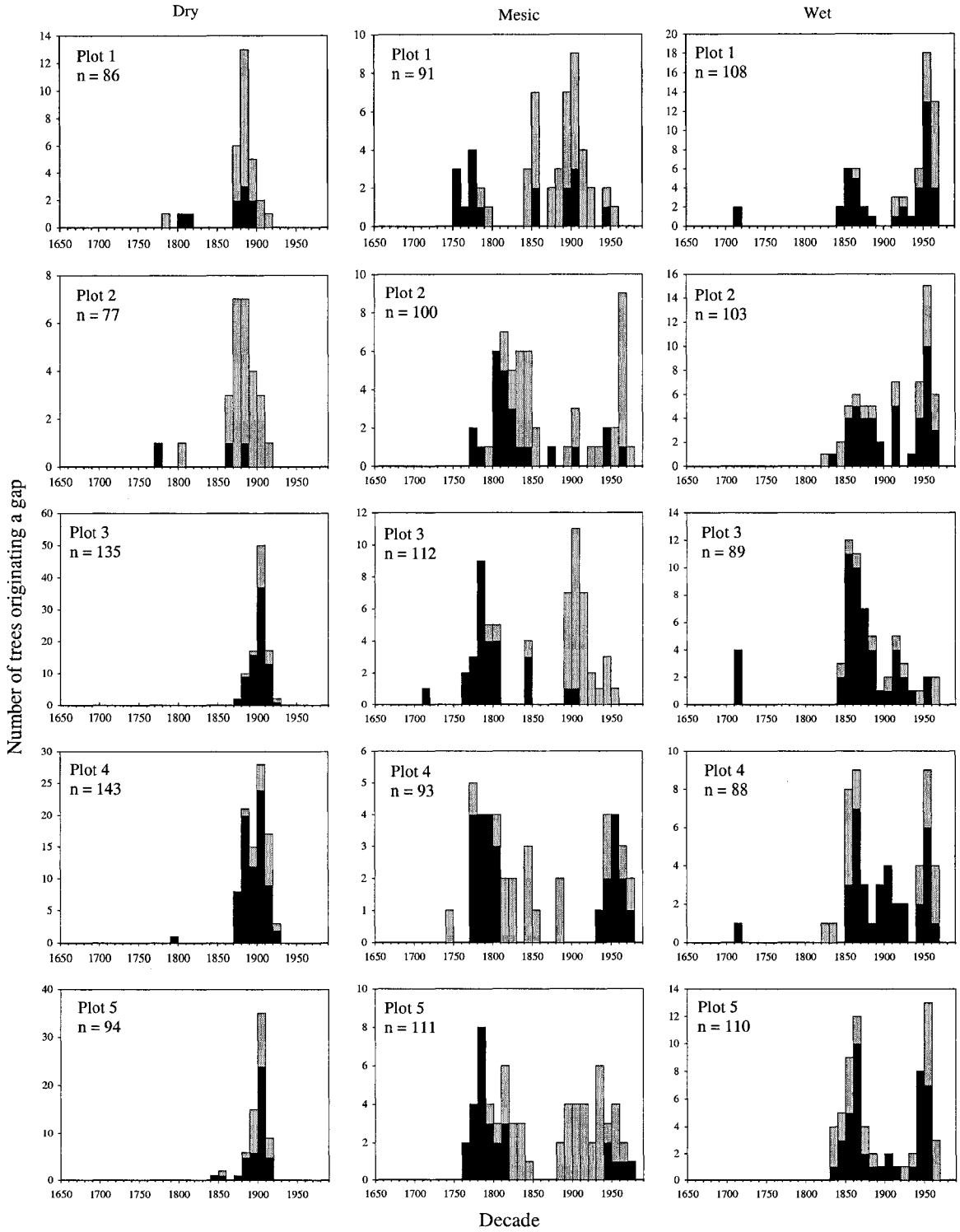

Figure 3.2. Frequency distribution of the number of spruce (black) and subalpine fir (grey) trees originating in a canopy gap within each decade for each plot. Plots are grouped as dry (left), mesic (middle) and wet (right) variants.

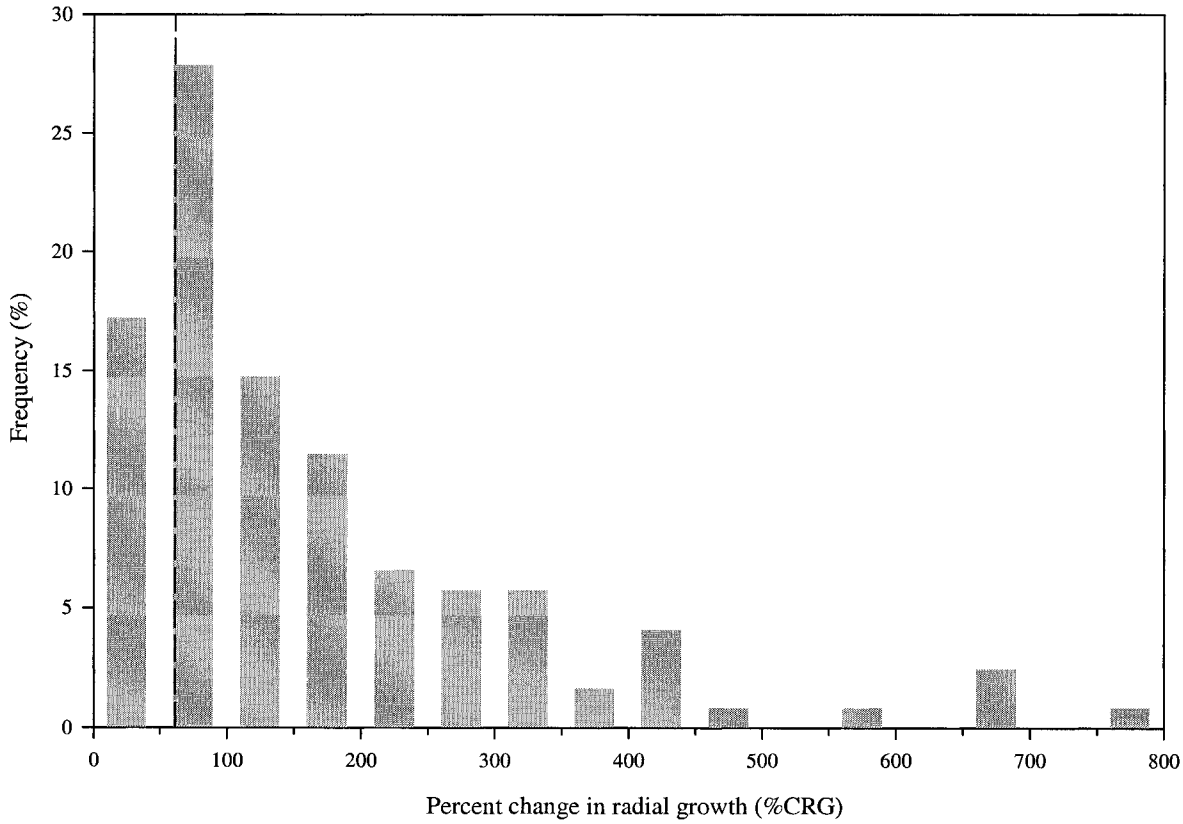

Figure 3.3. Frequency distribution of percent release for gap-fillers, pooled by species and ecological variant. Dotted line indicates the release criteria (25^{th}-Percentile = 60%). n = 117.

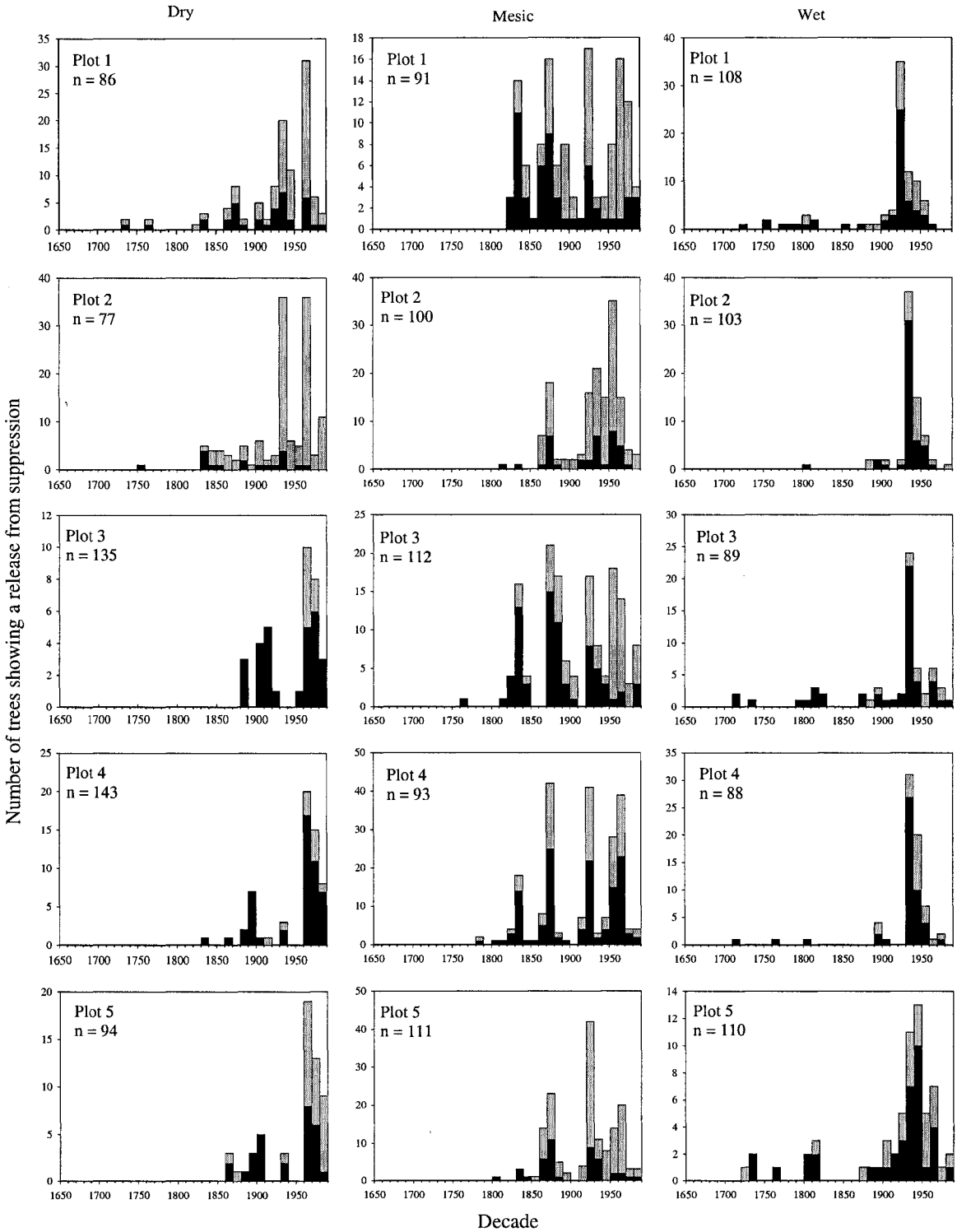

Figure 3.4. Frequency distributions of the number of spruce (black) and subalpine fir (grey) releasing from suppression within each decade for each plot. Plots are grouped as dry (left), mesic (middle) and wet (right) variants.

CHAPTER 4 - A NEW DENDROECOLOGICAL METHOD TO SEPARATE RESPONSES TO CANOPY TREE MORTALITY FROM CLIMATE

Abstract

As part of a larger project describing fine-scale disturbance within mature, spruce-fir forests within central British Columbia, release from suppression in response to canopy tree mortality was defined as >60 % change in radial-growth rates with respect to subsequent 15-year periods. This release criterion was calibrated using a sub-sample of gap-maker/gap-filler pairs with known years of mortality and response. Despite the conservative release criterion, analyses revealed that a substantial number of release events, attributed to climate, were being counted. In response, a new dendroecological method was developed using: (1) the species/regionally-specific cubic-spline chronologies, developed to emphasize regional growth trends for spruce and subalpine fir; and (2) gap-filler ring-width series, collected for spruce and subalpine fir to identify increases in radial growth as a response to the death of their corresponding gap-makers. The regional chronology was subtracted from each standardized gap-filler series producing a residual ring-width series for each gap-filler. One was added to each value of the residual series to avoid negative or erroneously large values when calculating percent divergence over time. Gap-filler percent divergence values were calculated as the percent change in residuals, centred on the year of death estimated for each gap-filler. The percent divergence criterion was set at a >15 % increase in residuals, with respect to subsequent 15-year periods.

Introduction[1]

Description and quantification of regional disturbance regimes is often based on the reconstruction of stand disturbance histories. Many techniques are available for reconstructing stand histories and each one is particularly suited for analyzing specific disturbance types. For example, in wet temperate regions with extended periods between coarse-scaled fires, the ages of the oldest trees may not be indicative of stand-initiation (Hawkes *et al.* 1997). In regions where uneven-aged stands with closed canopies and shade tolerant species are common, ages may also bear no meaningful relationship to the fine-scale disturbance history because disturbance is not a prerequisite for germination (Lorimer and Frelich 1989).

One of the fundamental dendroecological approaches for identifying disturbance events within uneven-aged stand types is the identification of release from suppression caused by the mortality of canopy trees. It is generally accepted that radial growth rates of previously suppressed trees will increase following removal of the canopy initiated by mortality, and that the release pattern is due to reduced levels of competition and increased resource availability (Lorimer and Frelich 1989, Abrams *et el.* 1995, Nowacki and Abrams 1997, Jones and Thomas 2004). Release is commonly defined as an event where the percent change in radial growth in a tree-ring series exceeds a given minimum threshold, such as 25, 50 or 100 %, which in some cases must be maintained for a certain length of time such as 5, 10 or 15 years (Lorimer and Frelich 1989, Payette *et al.* 1990, Nowacki and Abrams 1997, Black and Abrams 2004).

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[1] A version of this document will be submitted for publication under multiple authors. All data used in this study were collected by R. D. Thompson and a number of field and lab assistants. In this thesis I use 'we' and 'our' to reflect the involvement of others in various aspects of this work.

Lorimer and Frelich (1989) suggested that the identification of canopy disturbance based on release, measured as the percent change in radial growth, should be fairly accurate because uncertainty and ambiguity associated with the pattern is low. Ring-width series of gap-making trees, however, show a range of ring-width patterns prior to death, including slow decline resulting from root disease (Lewis 1997), to abrupt death of healthy trees with wide rings, resulting from windthrow or bark beetle outbreaks (Hard *et al.* 1983, Holsten 1984, Payette *et al.* 1990, Lewis 1997, Lewis and Lindgren 2002, Bleiker *et al.* 2003). When canopy trees decline before death, gap-filling trees may show complex or ambiguous growth patterns. When healthy canopy trees die suddenly, a more abrupt and sustained release within the ring-width series of gap-filling trees may result. Furthermore, the magnitude of release should differ considerably between these two types of disturbance, assuming that the magnitude in release corresponds to the magnitude of canopy removal. As a result, release criteria historically have been based on the magnitude of release expected after a specific disturbance type or they have been set with respect to goals of analysis, site, and species.

Veblen *et al.* (1991a), investigating the effects of major spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks, defined release as ≥250 % increase in mean radial growth rate when adjacent groups of 10 years are compared. In contrast, Nowacki and Abrams (1997) investigating relatively fine-scale disturbance histories of presettlement-origin oaks, defined release as ≥25 % increase in mean radial growth rate when adjacent groups of 10 years are compared. The application of different release criteria to one data set will result in substantial differences in the number of disturbance events identified (Rubino and McCarthy 2004). Varying the threshold used to identify a disturbance event will therefore have a large impact on characterization of historical disturbance regimes.

Disturbance is not the only factor influencing patterns of radial growth. According to the linear-aggregate model of radial growth, a ring width during a particular year is the result of a number of biotic and abiotic factors such as tree age, climate, endogenous and exogenous disturbances, anthropogenic influences on the environment, and measurement error (Fritts and Swetnam 1989). Release criteria are applied to individual ring-width series to partition the factors, particularly climate, from endogenous and exogenous disturbances (Lorimer and Frelich 1989). Despite the mathematical simplicity of identifying release, climatic variation can cause radial growth patterns that are identical to the release caused by mortality of neighbouring canopy trees, especially following extended periods of drought. As a result, an individual cannot be certain that a release, measured as a percent change in radial growth, is caused by disturbance. Lorimer and Frelich (1989) suggest that distinguishing release resulting from disturbance versus release from other factors is feasible primarily because the effects of the other factors generally do not persist as long as release from suppression caused by inter-tree competition. To account for variation in ring-widths caused by climate, yet permit the identification of past disturbance, the differentiation of climatic- versus disturbance-caused variation in radial growth is of utmost importance.

Release criteria have been used to describe the disturbance regimes for a diverse set of forest types, including eastern boreal forests (Bergeron and Charron 1994); temperate hardwood forests (Lorimer and Frelich 1989, Payette *et al.* 1990, Frelich and Graumlich 1994, Abrams *et al.* 1995); temperate coniferous forests of western North America (Zhang *et al.* 1999, Newbery 2001); and coniferous montane or subalpine forests (Veblen 1986, Veblen *et al.* 1991a, Veblen *et al.* 1991b, Veblen *et al.* 1994, Parish *et al.* 1999, Eisenhart and Veblen 2000). Despite the wide range of forest types examined, most of the disturbance histories quantified have focused on forests with closed canopies. This is not surprising, as

stand dynamics are known to have a profound effect on annual radial growth rates, including release from suppression, in closed canopy forests (Cook and Peters 1981, Phipps 1982, Rubino and McCarthy 2004). The development of dendroecological techniques, therefore, has been concentrated on the resource dynamics that occur when a closed canopy exerts strong influence over the growth of sub-canopy trees.

Understorey vegetation is often limited in closed-canopy forests. Further, understory establishment and recruitment into the canopy can be largely due to above- and below-ground resource dynamics resulting from recently dead or dying trees. For the most part, release from suppression results from changes in a tree's environment, such as increases in light or water availability following disturbance that removes or negatively impacts surrounding competitors (White and Pickett 1985, Rubino and McCarthy 2004).

Within central British Columbia, few disturbance histories have been reconstructed within the sub-boreal and subalpine forest ecosystems, which have relatively open canopies. It is unclear if the traditional release criteria of the literature are appropriate for use in these open-canopy forest types with unique stand structure, composition and light regimes. Although the light levels within sub-boreal and subalpine forested ecosystems are poorly quantified, there are a number of reasons to assume that light levels in these forest types are greater and less variable than in typical closed canopy stands. Furthermore, the light regimes of an open-canopy forest should result in differences in how understory trees establish, grow and eventually ascend into the canopy. Claveau *et al.* (2002) found that at <10 % full sunlight, eastern *Abies* and *Picea* species carried a higher live crown ratio, thus had larger crowns per unit of height than western species of the same genera. They hypothesized that the differences could be related to canopy tree composition and structure, where eastern species were under a canopy composed of deciduous species producing a closed canopy

forest, and western species were under a canopy composed of coniferous species producing an open canopy. This evidence suggests that the western genera are under less competition for light due to the open coniferous canopy.

Kneeshaw and Burton (1997) found that the canopies of most stands, within moist cool sub-boreal forests, were considerably open in their horizontal structure, with estimated canopy closure as low as 30.5 %. Coates (2000) found that seedlings of *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn. ex D. Don, *Abies lasiocarpa* (Hook.) Nutt., *Pinus contorta* var *latifolia* Engelm., *Picea engelmannii* × *glauca* Voss × Parry planted just off the canopy gap edge under canopy trees all performed poorly regardless of the cardinal direction from the gaps or gap size. This suggests that the assumed light advantage experienced off the north end of high latitude gaps, compared to other cardinal directions, is not necessarily beneficial for tree growth. Furthermore, their results suggest that below-ground resource dynamics may have an important influence on growth of sub-canopy trees within open-canopy forests. As canopy conditions become increasingly broken, light becomes less limiting.

Wright *et al.* (1998) found that saplings of *Abies amabilis* Dougl. ex Forbes *Abies lasiocarpa*, *Tsuga heterophylla*, *Tsuga mertensiana* (Bong.) Carr., *Thuja plicata, Pinus contorta* var *latifolia*, *Picea glauca* (Moench) Voss, *Picea engelmannii* Parry ex Engelm., *Picea engelmannii* × *glauca*, *Picea mariana* (Mill.) BSP, *Betula papyrifera* Marsh., *Populus tremuloides* Michx. and *Populus balsamifera* ssp. *trichocarpa* Torr. and Gray all had measurable radial and height growth rates even at the lowest light levels sampled in their study. Understory light levels in mature temperate and subalpine forests in the region rarely drop below five % full light (E.F. Wright and K.D. Coates, unpublished data, in Wright *et al.* 1998), unlike the much lower light levels (1-2 % of full sun) often found in broadleaf forests

of eastern North America or the tropics (Canham *et al.* 1990, Clark *et al.* 1996). Therefore, the radial growth of these coniferous species in high-latitude sub-boreal and subalpine forests appear to have fundamentally different responses to light than deciduous and coniferous species in broadleaf forests and lower latitude temperate forests (Pacala *et al.* 1994, Wright *et al.* 1998), where growth rates of most species sharply increase at very low light levels and can reach 50 % of maximum growth at light levels <10 % of full sun and near maximum growth at 20 % full sun (Fetcher *et al.* 1993).

The above literature suggests that understory light levels within sub-boreal and subalpine forests of central British Columbia can be abundant and relatively homogenous. Further, the importance of light as a limiting factor of growth within these ecosystems diminishes. As sub-canopy light levels increase, we expect that the importance of other growth factors, defined within the linear aggregate model, will increase. Most importantly, climate as a limiting factor may explain a greater proportion of variation in tree growth, introducing a new complexity when attempting to partition the effects of disturbance from climate. Further, release responses to the average fine-scale disturbance may diminish in magnitude with greater canopy openness, lowering the release threshold required to detect fine-scale disturbance and increasing the chance of interpreting climatic variation as evidence of overhead mortality.

With these important differences between the resource dynamics of open- versus closed-canopy forest types, there is an inherent problem associated with the application of traditional dendroecological techniques to forests with open canopies, despite being calibrated to account for the difference in forest composition and structure, or changes in the disturbance regimes that preside over the landscape (i.e., fine- vs. intermediate- to coarse-scale disturbance). That is, when we apply the same dendroecological techniques across

many regions, the level of uncertainty and ambiguity associated with the pattern of release from suppression is not constant. As a result, the error associated with the estimation of disturbance frequencies will change.

In previous work (Chapter 3), release from suppression caused by mortality of canopy trees was defined as ≥60 % increase in mean radial growth, when adjacent groups of 15 years are compared. This release criterion was applied to live *Abies lasiocarpa* and *Picea engelmannii* × *glauca* ring-width series from canopy trees ≥15 cm diameter at breast height (dbh, measured 1.3 m above the ground) sampled from sub-boreal and subalpine forests of central British Columbia. Numerous analyses revealed that the regional effect of (inferred) climate produced radial growth patterns identical to disturbance-caused release. Extended below-average growth rates, followed by a return to the average growth rate, triggered growth patterns identical to disturbance-caused release from suppression. Further, based on a comparison of decadal release frequencies (Chapter 3) and chronologies developed using horizontal-line standardization (Chapter 2), it was argued that the patterns were driven by climate rather than a regionally synchronous disturbance event. The horizontal-line chronologies did not reveal the dramatic and sustained release patterns that would be expected with synchronicity of release from suppression caused by major canopy disturbance.

Rozas (2001) found that standardized chronologies, developed from stands with either extremely low levels of past disturbance (control) or relatively high levels of past disturbance (affected), responded differently to standardization. By subtracting the affected chronologies from the control chronologies, the residual chronology could be used to date periods of coarse-scale disturbance. This suggests the individual standardized ring-width series, used to develop the chronologies within the disturbed stands, maintained a dendroecological signal

associated with canopy-removal. We hypothesize that standardized ring-width series that diverge from a co-located species/regionally-specific chronology – based on the same detrending method – could also be used to identify stand dynamics at fine-spatial scales (i.e., individual trees). The objectives of this study were to: (1) develop a new dendroecological method, based on divergence between chronologies, to separate fine-scale disturbances from regionally synchronous events; and (2) discuss how the divergence method adds to the traditional release method.

Methods

As part of a larger research project intended to characterize the fine-scale disturbance regimes in spruce-subalpine fir dominated forests within central British Columbia three biogeoclimatic variants were selected. The Stuart Dry Warm Sub-Boreal Spruce (SBSdw3), Willow Wet Cool Sub-Boreal Spruce (SBSwk1) and Misinchinka Wet Cool Engelmann Spruce-Subalpine Fir (ESSFwk2) biogeoclimatic variants are located in two of the most common biogeoclimatic zones located in central British Columbia. The SBSdw3, SBSwk1 and ESSFwk2 variants will be referred to as the dry, mesic and wet variants, respectively. Within each variant, five spruce-subalpine fir stands were selected and within each stand one 0.25-ha (50-m × 50-m) plot was randomly placed, for a total of 15 plots.

Calibrating percent divergence

The following method uses (1) the species/regionally specific cubic-spline chronologies, developed in Chapter 2, to emphasize regional radial growth trends for spruce and subalpine fir, and (2) the gap-filler ring-width series, collected in Chapter 3 for spruce and subalpine fir from each variant, to identify release events as responses to the death of

their corresponding gap-makers. Examples of these data are presented in Figures 4.1a – c. We assumed that the gap-filler ring-width series, in response to the death of their corresponding gap-maker, would diverge to some degree from the regional trend for a given length of time. Gap-filler ring-width series were compared against their co-located regional chronology to identify periods where radial growth diverged from the regional growth trend. Using the same standardization method used to develop the chronologies, each gap-filler series was fit with a cubic-spline of 50 % frequency response of 50 years (Figure 4.1c) and ring-width indices were calculated by division (Figure 4.1d). The regional chronology was then subtracted from each standardized gap-filler series (Figure 4.1e) producing a residual ring-width series. One was added to each value of the residual series to avoid negative or erroneously large values when calculating percent divergence over time. Percent divergence was calculated for the residual series based on the year of death estimated for each gap-filler as,

$$[1]\ Percent\ Divergence = \left(\frac{MDA_{15} - MDB_{15}}{MDB_{15}} \right) * 100$$

where:

MDB_{15} = 15-year residual mean before the gap-maker year of mortality; and

MDA_{15} = 15-year residual mean after and including the gap-maker year of mortality.

Fifteen-year periods before and after the gap-maker year of mortality were used to maintain consistency with the original release threshold developed in Chapter 3. As the residual series is the result of the regional chronology being subtracted from each standardized series, erroneous residuals can result when subtracting the regional chronology in years where it is represented by too few samples ($n < 5$). To avoid this, calculation of the residual series

began when the regional chronology sampling depth was ≥ five, and the calculation of percent divergence began 15 years thereafter (Figure 4.1b, e, and f).

Gap-filler percent divergence values were plotted against the original gap-filler percent release values, and correlated (SPSS Inc. 1999, Tabachnick and Fidell 2001). Differences in the levels of percent divergence by species and by ecological variant were tested using a nested ANOVA with species nested within variant (Zar 1996, SPSS Inc. 1999). Explanatory variables in the nested ANOVA were treated as random effects. To maintain consistency with the original release threshold calibration methods, the number of unique percent divergence criteria was based on any differences found in the ANOVA. Further, the 25^{th}-percentile of the gap-filler percent divergence values was used as the divergence threshold.

Application of the divergence method

Within each plot, all living trees ≥15 cm dbh were cored at breast height. Cores were prepared, measured and cross-dated following standard dendrochronology techniques (Stokes and Smiley 1968, Holmes 1983). Once the ring-width series were dated, yearly percent divergence values were calculated for each canopy tree (Figure 4.1f).

A comparison of the yearly percent divergence and yearly percent release identifies four possible outcomes (Figures 4.1f and 4.1g). First, the release and divergence criteria are both met. Second, the release and divergence criteria are both not met. Third, release is met while divergence is not. Fourth, divergence is met while release is not. Physiologically, we assume that if a canopy disturbance had occurred in the past and an understory tree was there to ascend towards the canopy, the understory tree would have shown a release pattern. Furthermore, the release pattern would likely have met the release threshold defined in

Chapter 3. To be confident, however, that a release event was indeed caused by fine-scale disturbance, and not some other regionally synchronous event (e.g., climate), the release event was only counted if the divergence threshold was also met. It is unlikely that the calculations would result in the two criteria being met during the same year; therefore, the release and divergence criteria had to be met ± five years of one another. The amalgamated "release and divergence" criterion will now be referred to as the divergence method.

Analyses of the divergence method

To compare the number of disturbance events identified by the divergence method against the number of events originally identified by the release method (Chapter 3), decadal frequency distributions of release (Chapter 3, Figure 3.4) and divergence were calculated for each species, within each plot. Plot level frequency distributions of divergence were not plotted, but were used in the following methods. The number of release events was subtracted from the number of divergence events, giving the total number of release events removed per decade. The resulting value was negative if release events were removed. These events were determined to be caused by a regionally synchronous event. The number of release events and the number of release events removed per decade were pooled by variant.

To assess the relationship visually between the species/regionally-specific chronologies and the frequency of release events identified and the frequency of release events removed per decade, the chronologies were plotted with the decadal frequency of release events identified and removed per decade.

To assess the relationship between the species/regionally-specific chronologies and the proportion of release events removed at the plot level, the proportion of release events

removed per decade was plotted against the decadal ring-width index. The decadal ring-width index was calculated by averaging the ring-width indices for each decade. The proportion of release events removed per decade was calculated separately for spruce and subalpine fir, by dividing the number of release events removed per decade by the sample size of each species within each plot.

The divergence method was based on the assumption that a negligible proportion of fine-scale disturbance events would be removed during any period where the species/regionally-specific chronology showed average growth rates. Conversely, if the regional chronology showed an extended period of below average growth, followed by a return to average growth, it was assumed that a substantial proportion of release events would be removed. With extended and/or more severe periods of below average growth we expected that the proportion of release events removed would increase exponentially because release patterns would become common to a majority of the sample trees. Further, the pattern of release would be maintained as ring-width variation within the species/regionally-specific chronology. To test this hypothesis, nonlinear regression was used to fit a two-parameter negative-exponential curve to the scatter plot of the proportion of release events removed per decade versus the mean decadal ring-width index (SPSS Inc. 1999, Zar 1996).

Results

Calibrating percent divergence

Gap-filler percent release and percent divergence values were positively correlated (Figure 4.2). Thirty of the original 117 gap-filler samples had divergence values < zero, despite all showing positive release (Figure 4.2). Based on the uncertainty that these samples represent the population of gap-filling trees, we excluded these values from further analyses.

Seventy-two of the 87 gap-fillers with positive divergence values had release values > 60 % (Figure 4.2).

After the negative percent divergence values were removed, the distribution of percent divergence was positively skewed (Figure 4.3). To meet the ANOVA assumptions of normality and homogeneity of variance, the data were transformed using the Box-Cox transformation (Sokal and Rohlf 1995). ANOVA results detected no significant differences in percent divergence between ecological variant (Table 4.1) or between species nested within variant (Table 4.1). Based on these results, one unique percent divergence threshold was selected based on the pooled data for spruce and subalpine fir across all three ecological variants (Figure 4.3). Fifty percent of the observations for percent divergence fell between 15 % and 42 % with the median being 25 %. Based on the 25^{th}-percentile, a 15 % divergence from the regional chronology was chosen to represent a disturbance at a fine-spatial scale (i.e., the individual tree) (Figure 4.3).

Application and analyses of the divergence method

Despite the coarse temporal scale of the number of release events removed in each decade, qualitative analysis of Figure 4.4 suggests a moderately consistent pattern. The largest frequency of release events removed in each decade coincides with decades of growth suppression (Figure 4.4). One exception occurred within the dry (early) variant where growth suppression was followed by increased growth rates and a period of positive growth, resulting in consecutive decades of release removal (Figure 4.4). It is also apparent that some original release events were moved into adjacent decades because both divergence from the regional chronology and percent release ≥60 % could be met ± five years of each other (Figure 4.4). The association between the proportion of release events removed in each

decade and the mean decadal growth index was not extremely strong, however, the regression is significant, suggesting that if the regional chronology showed an extended period of below average growth, followed by the return to average growth, a greater proportion of release events would be removed (Table 4.2 and Figure 4.5).

Discussion

Objective criteria are needed for identifying radial growth patterns that represent radial growth release in a gap following the death of a canopy tree. This study has outlined a dendroecological method to do so. The results of this study demonstrate that the divergence method is better than traditional release methods with regard to its ability to separate responses to fine-scale disturbance from regionally synchronous events (e.g., climate) within sub-boreal and subalpine forests of central British Columbia.

Black and Abrams (2004) argue that even if the effects of age, size, or climate are quantified and taken into account, the utility of radial growth criteria (i.e., release criteria) is still not optimized unless a single, standardized method is developed. Numerous release criteria have been employed, each specific to investigators' research goals, selected sites, species, and disturbance regimes (Black and Abrams 2004, Rubino and McCarthy 2004). These authors argue that without standardized criteria, direct comparisons among these studies are complicated. We suggest, however, that it is not the lack of a standardized method that diminishes the potential power of dendroecology to quantify disturbance patterns across diverse landscapes or regions, but the lack of a standardized way of assessing the varying levels of error associated with each new growth rate criteria. This study, in combination with previous work (Chapters 2 and 3), suggests that the application of standardized growth rate criteria to different data sets, from distinct regions, results in

considerable changes to the counting errors associated with the identification and quantification of disturbance.

Two types of error can occur when applying release criteria to assess canopy disturbance, and an analogy can be drawn from the relationships between hypotheses and decisions made in statistical hypothesis testing (Table 4.3). A type I error is committed when a canopy release is identified but there is no coincident death of a canopy tree. In this case, a growth release may occur but is caused by climate variation or a disturbance other than the formation of a canopy gap. A type II error is committed when release occurs following the creation of a canopy gap, but the release is not detected. In this case, the magnitude of the release may be too small to be detected. To extend the analogy further, the power associated with a given growth rate criterion can be defined as the ability of the criterion to detect a growth release when a canopy tree dies and creates a gap. With this in mind, by selecting "liberal" release criteria, disturbances would be identified more often than they actually occur, decreasing type II errors and increasing the power of the test, but also increasing the number of type I errors. In contrast, by selecting "conservative" release criteria, disturbances would be identified less often than they actually occur, decreasing type I errors, but decreasing the power of the test and increasing the number of type II errors.

In Chapter 3, the release threshold was set at a percent change in radial growth $\geq$60 %. With this release threshold, there was a high likelihood that a release event would be identified when an overhead mortality event truly did occur. Despite the power associated with the release threshold, however, many type I errors occurred because both climate and disturbance result in similar ring-width patterns that are difficult to differentiate using historical reconstruction techniques. One option to decrease the frequency of type I errors

would be to increase the magnitude of release required to identify overhead mortality. This solution, however, would be at the cost of increased type II errors and decreased power.

A second option to decrease the frequency of type I errors would be to increase the "adjacent groups of 15 years compared" to adjacent groups of 20 or 25 years. To do so, requires the recalibration of the original gap-maker/gap-filler pairs. This would have decreased the release threshold below 60 %, because an increased number of years used to calculate growth rates before and after any given year has a higher likelihood of bringing before and after growth rates closer to the mean ring-width for the entire period used in release calculation. The before and after mean growth rates for each canopy tree sampled, however, should also have the same likelihood of being closer to the mean ring-width for the entire period used in release calculation. The mean growth rate after the year of disturbance is, therefore, less likely to be much greater than the mean growth rate before disturbance. Theoretically, there is a counter-balancing effect by increasing the number of years used to calculated mean growth rates before and after a given date. Therefore, no substantial shift in error types from the origin levels should occur.

The above options maintain unacceptable levels of error and justify the addition of the divergence criteria to the original release criteria. Although this is highly conservative, by combining the two criteria, the frequency of type I errors caused by regional-scale variation (e.g., climate) have been decreased considerably. The cost of increased type II errors and reduced power associated with the reduced frequency of type I errors, however, remains uncertain. Figures 4.4 and 4.5 both show a small number or proportion of release events being removed in a number of decades where it is not expected because we assumed that a negligible proportion of true disturbance events would be removed during any period where the regional chronology showed an average or above average ring-width indices. Although

the divergence and release thresholds had to be met ± five years of each other to count as a canopy disturbance event, and it was possible for some of the original release events to be moved into adjacent decades, it does not account for all of the unexpected release events removed during periods where the regional chronology showed average or above average ring-width indices.

The most plausible explanation would simply be that the release threshold was met while divergence was not. This is illustrated where a small or negative percent divergence values are possible over a wide range of percent change in radial growth values (Figure 4.2). It is possible that these removed release events are disturbance related. It is difficult, however, to say whether the response was caused by overhead mortality or a response to the death of an adjacent canopy tree. In addition to the release of understory trees by the death of an overhead tree, growth increases in existing canopy trees do occur in response to the death of adjacent canopy trees (Frelich and Martin 1988, Lorimer and Frelich 1989, Pedersen and Howard 2004). Lorimer and Frelich (1989) suggest that the frequency of disturbance in a given decade can be overestimated by the addition of the amount c/N, where c is the number of sample trees showing a canopy thinning response in that decade and N is the total number of sample trees in the plot. If these responses are the result of adjacent canopy tree mortalities, then it is preferable to eliminate such responses. These thinning responses could also be removed by using age, size, growth and/or distance criteria in the year a tree showed release. For example, Newbery (2001) found that only trees >20 cm dbh caused release when they died, and understory trees were typically < five m from the dead canopy tree, they were at least five cm dbh less than the dead tree and they were of vigorous growth.

Coincidentally, the divergence criterion also removes intermediate- to coarse-scale disturbance events that are regionally synchronous. Depending on the research question, this

may or may not be considered a type II error. With regard to the larger project objectives – the characterization of fine-scale disturbance regimes in central British Columbia – this is not an error because the goal was to estimate the frequency of fine-scale disturbance. In fact, it can be considered the partitioning of intermediate- to coarse-scale, regionally synchronous disturbance events, from fine-scale disturbance events. In Figure 4.4, both the mesic (ca. 1870s) and wet (ca. 1930s) variant plots have a period where the relative slow growth is not climate driven, but a product of standardization using a cubic-spline that is not flexible enough to conform tightly to the common, dramatic and sustained patterns of release expected within individual ring-width series after a disturbance event that removes much of the canopy (Veblen *et al.* 1991a, 1991b). The interpretation of this phenomenon is justifiable, and illustrated for a spruce ring-width series selected from the mesic variant (Figures 4.1c and d). In this example, the spline diverges prior to the 1870s abrupt and sustained release. This results in ring-width indices consistently less than one just before the release. If this trend is consistent within most canopy trees across an entire region, then the regional trend will express negative ring-width indices followed by increasing growth rates. Furthermore, when calculating the residual series, series will not show a divergence pattern from the regional trend, thus partitioning regionally synchronous disturbance events from fine-scale events.

The final criticism of the divergence method is not necessarily related to error type, but is concerned with the inherent limitations placed on the maximum disturbance chronology length. The new method truncates the disturbance chronology length because the calculation of residual series begins when the sampling depth of the regional chronology is $\geq$ five, and the calculation of percent divergence can only begin 15 years thereafter. Substantial stem decay at coring height, loss of older trees through natural mortality, and the

destruction of young or mature stands as a result of intermediate- and coarse-scale disturbance can all reduce the apparent intensity of past disturbance (Lorimer and Frelich 1989). Furthermore, Lorimer and Frelich (1989) suggested that the loss of evidence from earlier disturbance should be addressed by restricting disturbance chronology length to a period of time where the evidence loss rate is fairly small. Average residence time of canopy trees is a common value used to determine reasonable chronology length. In the absence of stand-replacing fire, residence time within the sub-boreal and subalpine forests within this study are often over 200 years (Chapter 2, Figure 2.2). The limitations placed on the disturbance chronology lengths by the divergence calculation, however, ranged from 100 to 200 years (Figure 4.4). Therefore, the calculation of divergence places a reasonable limit on chronology length.

In conclusion, the divergence method is not without error. By combining the new divergence criteria with the original release criteria, however, the frequency of type I errors, caused by regional-scale variation (e.g., climate), have been decreased considerably, without a great cost of increased type II errors and reduced power. Furthermore, the results show that standardizing release criteria should not necessarily be the solution to direct comparisons of disturbance regimes across different regions. It is clear that, despite their final objective use, all growth-rate criteria will continue to maintain a level of error in the identification of disturbance. Whether the criteria are calibrated to account for the effects of age, size, or climate, or whether a completely new technique is developed to identify disturbance, all criteria generally have a minimized, yet misunderstood and accepted level of uncertainty. Without a standardized way of assessing the varying levels of error associated with each new growth rate criteria, direct comparisons of disturbance regimes across different regions will continue to be a complex issue.

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Table 4.1. Nested ANOVA results of percent divergence values between ecological variant and between species nested within ecological variant.

Source	SS	df	MS	F	p
Variant	2.766	2	1.383	0.182	0.842
Species (Variant)	22.806	3	7.602	1.762	0.161
Error	349.410	81	4.314		

Table 4.2. Nonlinear regression statistics for proportion of release events removed in each decade against the mean decadal indices for each regional chronology using two parameter negative-exponential function where $f(x) = 11.053 \times e^{(-5.596 \times x)}$.

Source	SS	df	MS	F	p
Regression	1.013	2	0.507	101.4	<0.001
Residual	0.793	152	0.005		
Total	1.806	156			
Corrected	1.083	155			
Raw R^2	0.561				
Adjusted R^2	0.268				

Table 4.3. Conceptual framework identifying the two error types during the identification of release.

	Overhead mortality event did not truly happen	**Overhead mortality event did truly happen**
Release not identified	No error	Error type II
Release identified	Error type I	No error (power)

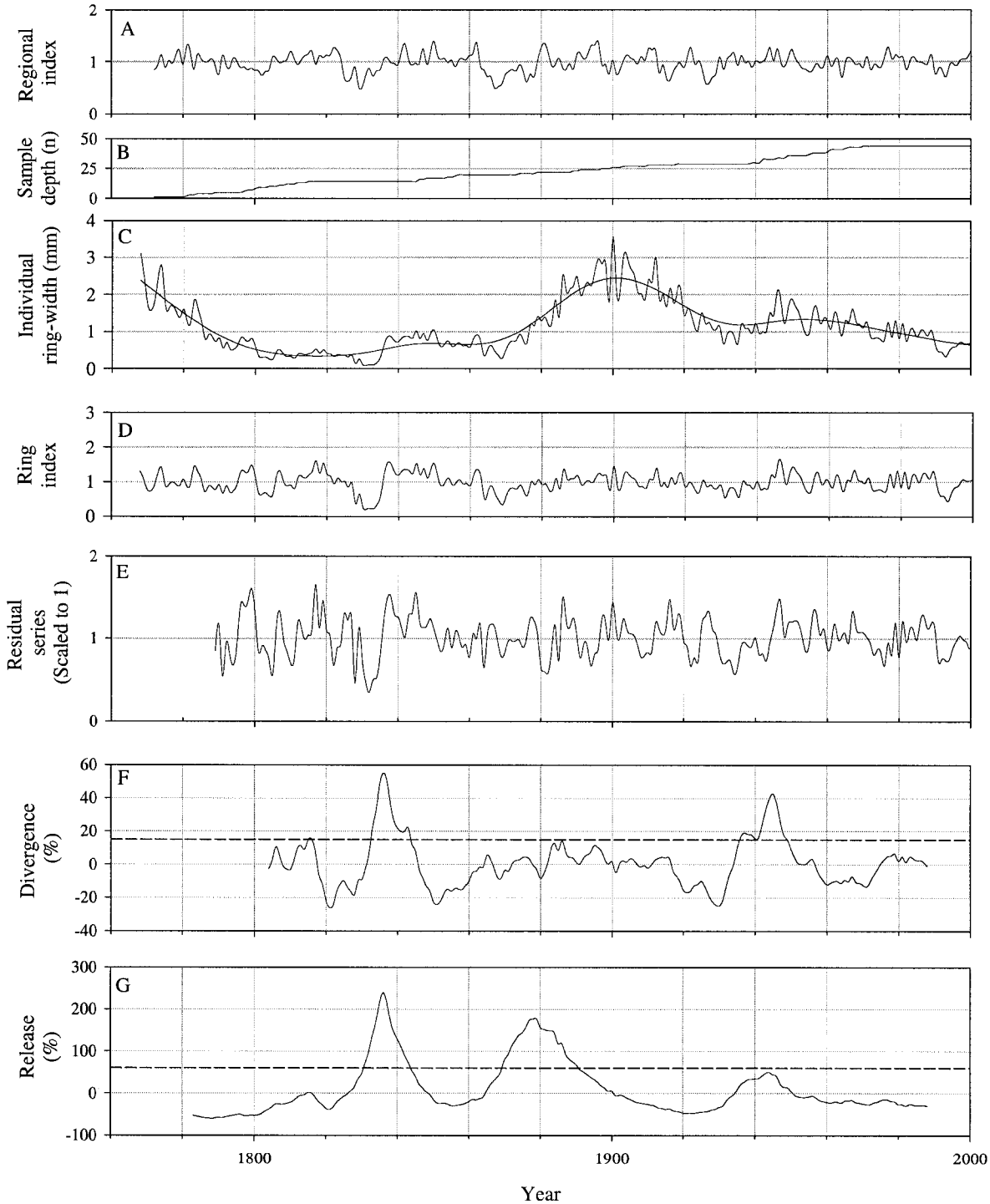

Figure 4.1. Pictorial outline of the divergence method used to identify responses to overhead canopy mortality events. In graph C, the individual ring-width series is fit with a cubic-spline of 50 % frequency response of 50 years. Dashed lines in graph F and G represent the 15 % divergence and 60 % release thresholds, respectively.

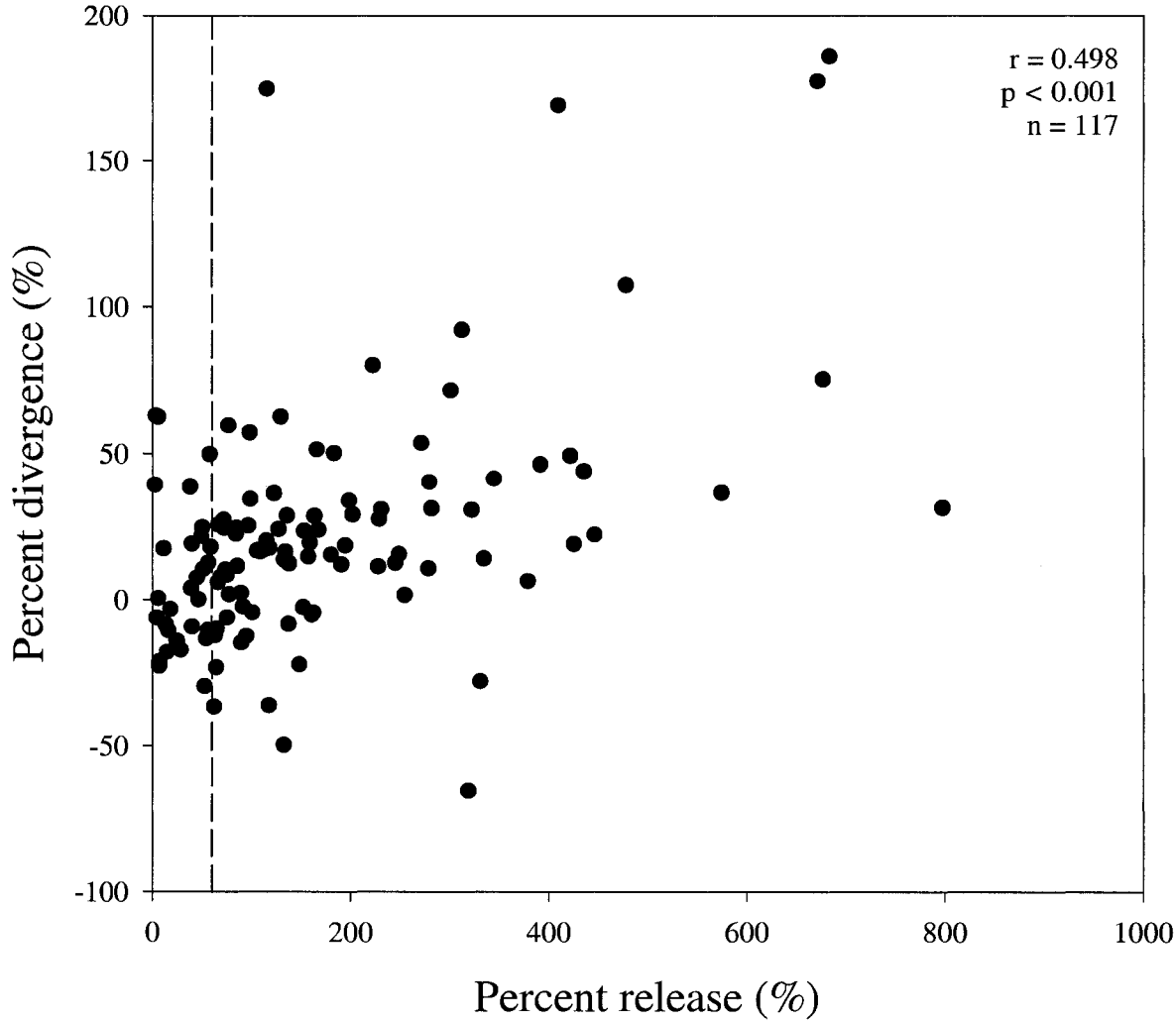

Figure 4.2. Gap-filler percent divergence values versus percent release values. The dashed vertical line indicates the 60 % release threshold.

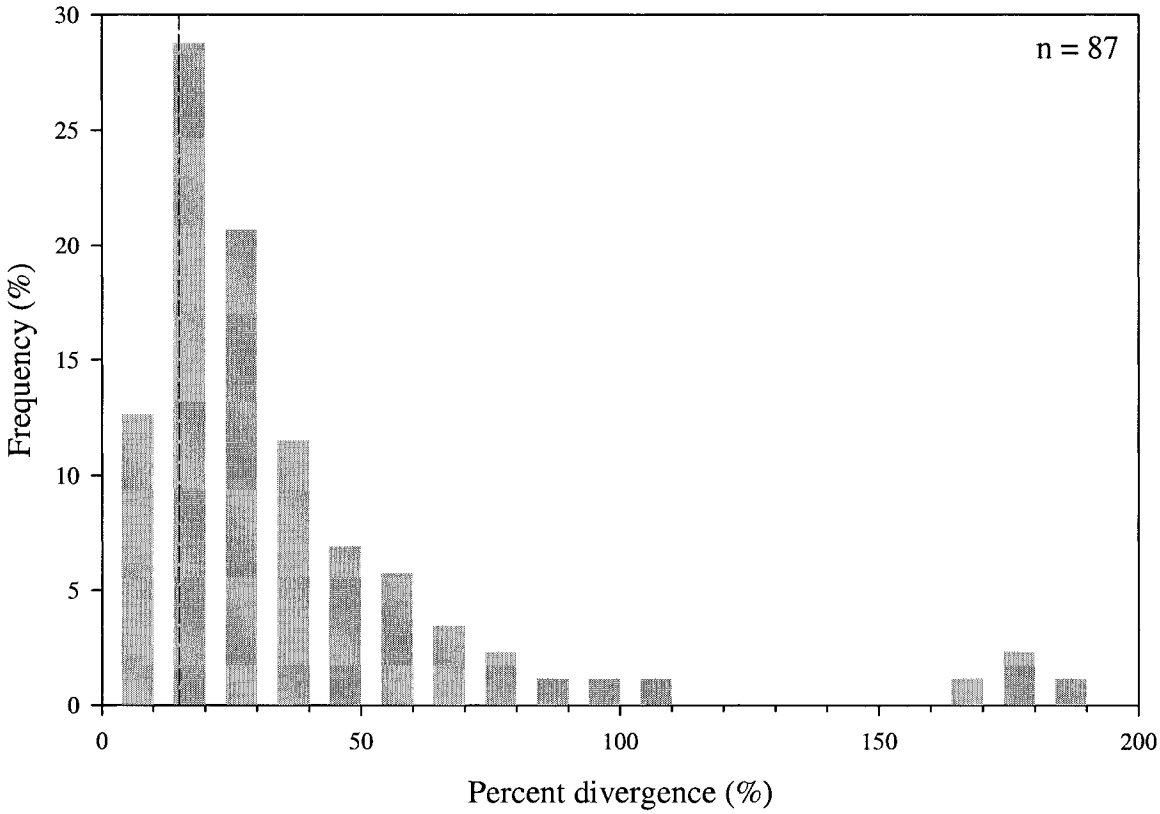

Figure 4.3. Frequency distribution of gap-filler percent divergence values. The dashed line indicates the divergence threshold (25^{th}-percentile = 15%).

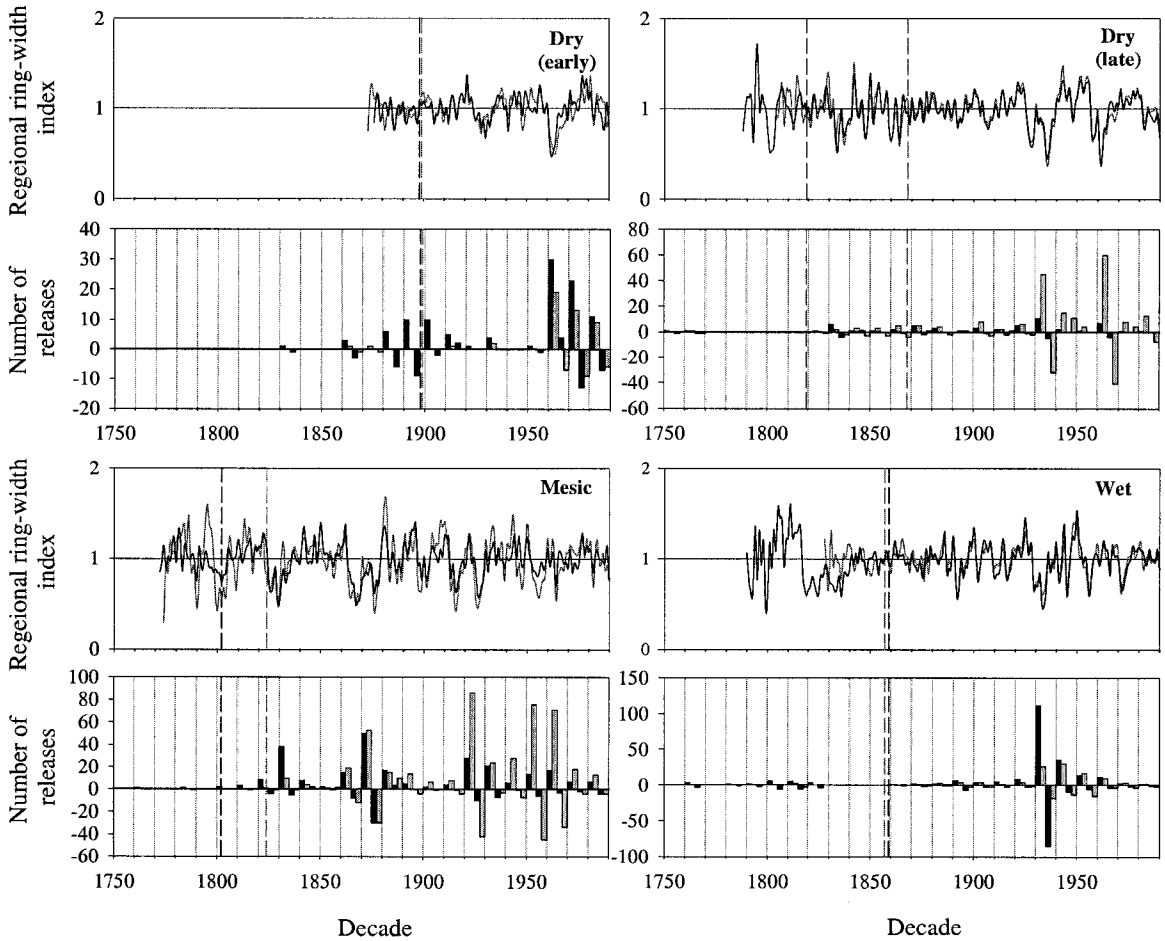

Figure 4.4. Regional chronologies (upper plot) compared with frequency of release events original identified and the frequency of release events removed by the divergence method (lower plot) in each decade. Black and grey lines and bars represent spruce and fir, respectively. Dashed vertical lines indicate 15 years after the species/regionally specific chronology is represented by ≥ five samples. Within the lower plots, four bars are presented per decade. The first two bars represent release events identified and the second two bars represent the number of releases removed by the divergence method.

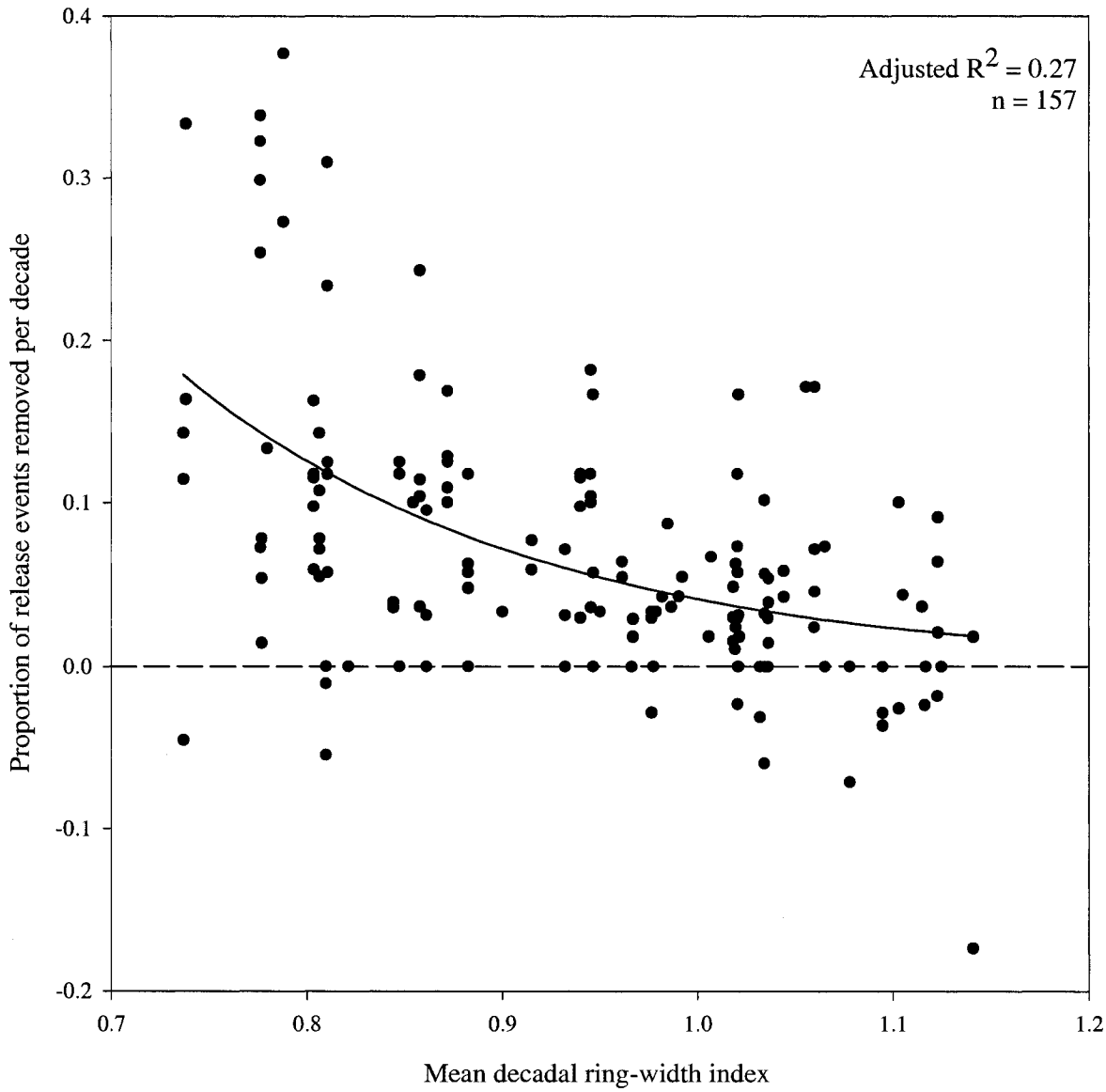

Figure 4.5. Relationship between the proportion of release events removed and the mean regional decadal ring-width indices. The proportion of release events removed in each decade was regressed against the mean decadal indices for each regional chronology using two parameter negative-exponential function where $f(x) = 11.053 \times e^{(-5.596 \times x)}$.

CHAPTER 5 – FINE-SCALE SPATIO-TEMPORAL DISTURBANCE PATTERNS IN MATURE, SPRUCE-SUBALPINE FIR FORESTS FOUND IN THE CENTRAL INTERIOR OF BRITISH COLUMBIA

Abstract

Within central British Columbia fire is viewed as the primary disturbance influencing forest dynamics. Although these forests do originate by fire, times between stand-replacing events are enormously varied. With increasing time between stand-replacement, fine-scale disturbance can assume an important role in forest dynamics. To characterize fine-scale disturbance regimes across central British Columbia three ecosystems were selected: dry sub-boreal, mesic sub-boreal and wet subalpine. Within each ecosystem, five 0.25-ha plots were located in mature, spruce-subalpine fir forests. Growth rate criteria were used to date ascensions towards the canopy caused by the creation of canopy gaps resulting from the death of canopy trees. Moran's I analysis of ascension dates suggests that disturbance is random in space and time. Canopy openings caused by disturbance averaged ≈2.5 m in diameter. Decadal disturbance rates did not differ by variant ($p = 0.117$) or by species nested within variant ($p = 0.418$). Although the decadal disturbance rates did not differ by variant, mean rates within dry, mesic and wet ecosystems were 7.4, 6.4 and 5.0 %, respectively. The consideration of disturbance at multiple scales suggests that fine-scale disturbance exhibits continuous stand level maintenance and renewal; however, notable compositional changes in species dominance tend to be abrupt and due to intermediate- and coarse-scale disturbances.

Introduction[1]

The vital role of intense, coarse-scale stand-replacing fire in boreal, sub-boreal and sub-alpine forests of western North America has long been acknowledged (Johnson and Rowe 1977, Hawkes 1980, Romme 1980, Heinselman 1981, Pyne 1984). Recently, sub-boreal and subalpine forest ecosystems within the central interior of British Columbia have been receiving greater attention with regard to similar catastrophic events (Andison 1996, DeLong and Tanner 1996, Hawkes *et al.* 1997, DeLong 2000). As a result, historical fire regimes in central British Columbia are seen as largely responsible for the patterns we see today on the landscape. In regions where fire plays a critical role in mediating forest dynamics, stand-replacing fires generally come at intervals less than tree longevity (Johnson 1992). If so, fine-scale disturbance processes caused by the fall of single or multiple trees should have little influence on long-term forest dynamics because several tree generations do not pass between intense disturbance events.

Sub-boreal and subalpine forest stands, in most cases, do originate by fire. Recent studies, however, suggest that the times between these intense, coarse-scale stand-replacing events are enormously varied within central British Columbia (Hawkes *et al.* 1997, Sanborn *et al.* 2001). Within this study, we assume that much of this variation is linked to the climatic gradient that spans from the dry-warm interior plateau to the wet-cold foothills of the Canadian Rockies. In progressively wetter ecosystems, fire may become so infrequent that the development of true old-growth forests may be the norm (see Oliver and Larson 1996). Hawkes *et al.* (1997) report that fire-return intervals in very wet and cool sub-boreal and

[1] A version of this document will be submitted for publication under multiple authors. All data used in this study were collected by R. D. Thompson and a number of field and lab assistants. In this thesis I use 'we' and 'our' to reflect the involvement of others in various aspects of this work.

subalpine forests near the Rocky Mountains likely range from 1200 to 6250 years. DeLong and Tanner (1996) reported return intervals ranging from 227 to 345 years in slightly drier sub-boreal forests in the foothills of the Rocky Mountains. With increasingly greater time periods between stand-replacing events, fine-scale disturbance events can assume an important role in long-term forest dynamics. These disturbances, caused by a collection of biotic and abiotic agents, may maintain and renew the forest structure in stands with long fire-return intervals (Lewis and Lindgren 2000, Newbery 2001).

An extensive body of literature describes fine-scale disturbance patterns and processes in numerous forest types, including tropical (Denslow 1987, Lawton and Putz 1988), temperate North-American (Runkle 1984, Lorimer *et al.* 1988, Lorimer and Frelich 1989, Payette *et al.* 1990, Frelich and Graumlich 1994, Abrams *et al.* 1995), eastern boreal and sub-boreal (Bergeron and Charron 1994, Frelich and Reich 1995, Kneeshaw and Bergeron 1998), western coastal (Canham 1988, Lertzman *et al.* 1996, Brett and Klinka 1998, Daniels 2003) and coastal subalpine forests (Lertzman and Krebs 1990, Lertzman 1992, Lundquist and Beatty 2002).

An emerging body of literature suggests that fine-scale disturbances within central British Columbia can play an important role in stand-level forest dynamics (Kneeshaw and Burton 1997, Lewis and Lindgren 1999, Newbery 2001, Antos and Parish 2002a, Antos and Parish 2002b). Much of the work, though, has been dedicated to describing gap size or shape, and its influence on tree regeneration dynamics (Kneeshaw and Bergeron 1997, Wright *et al.* 1998a, Wright *et al.* 1998b, Eastham and Jull 1999, Coates 2000).

Across the climatic gradient from the dry-warm interior plateau to the wet-cold foothills of the Canadian Rockies, we expect that fine-scale disturbance events vary greatly in spatial scale and frequency. One common feature across the gradient is the existence of

spruce-subalpine fir forest types. As part of the ecosystem classification system used in British Columbia, Meidinger and Pojar (1991) suggest that similar climax vegetation can occur over a range of ecological systems. Similar climax forest communities can represent ecosystems from completely different regional climates and disturbance regimes, or similar regional climates and disturbance regimes can lead to differences in climax communities. Although forest ecosystems may be similar in their constituent species, considerable differences in the fine-scale disturbance types are expected. The objectives of this study were to describe and compare the spatial and temporal patterns of fine-scale disturbance in mature, spruce-subalpine fir forests found across the central interior of British Columbia. These objectives were addressed by developing canopy tree stem-maps, analyzing species structure and composition, and the assessing the spatial-temporal patterns of disturbance.

Methods

Field sampling

We selected three biogeoclimatic variants to represent the climatic gradient that spans the dry-warm interior plateau to the wet-cold foothills of the Canadian Rockies (Chapter 1, Figure 1.1). The Stuart Dry Warm Sub-Boreal Spruce (SBSdw3), Willow Wet Cool Sub-Boreal Spruce (SBSwk1) and Misinchinka Wet Cool Engelmann Spruce-Subalpine Fir (ESSFwk2) biogeoclimatic variants are located in two of the most common biogeoclimatic zones located in central British Columbia. The SBSdw3, SBSwk1 and ESSFwk2 biogeoclimatic variants will be referred to as the dry, mesic and wet variants, respectively.

Within each variant, we selected five forest stands. Stands were selected using several criteria. First, forest stands were beyond the stem exclusion stage as defined by Oliver and Larson (1996). This criterion was used to select stands in which trees were

establishing in the understorey and, in the absence of stand-replacing disturbances, were advancing toward the true old-growth stage of development (Oliver and Larson 1996). Second, forest soils had intermediate soil moisture (mesic) and nutrient (mesotrophic) regimes (Meidinger and Pojar 1991). This criterion was intended to minimize variation in tree species growth characteristics and disturbance processes as a result of highly divergent edaphic influences of soil moisture and nutrients. Third, forest stands had a mixture of spruce and subalpine fir as the dominant component of the canopy, with basal area >80 %, for all trees over 15 cm diameter at breast height (dbh, measured 1.3 m above the ground). A common tree composition and density minimized variation in stand susceptibility to disturbance. Finally, forest stands had no evidence of industrial forest activities. This final criterion ensured that stand dynamics resulted from natural disturbances, which may include past traditional uses and practices of First Nations. Consequently, stands are not representative of the average of the biogeoclimatic variant, but rather, they are typical of stands satisfying the criteria within each variant.

Within each stand, one 0.25-ha plot was located by randomly placing the south-western plot corner, which was defined as the plot origin (0, 0 m), for a total of 15 plots. From the plot origin, plot boundaries were defined by a 50-m x 50-m closed traverse along each cardinal bearing. At each plot corner and traverse midpoint (i.e., 25 m), stakes were placed and numbered one to eight.

For all living and dead trees with dbh >15 cm, we mapped the x and y coordinates relative to the plot origin. All coordinates were calculated using two azimuths taken from any two adjacent stakes with a 25-m base and related back to the origin using trigonometry. Stems were numbered, species tallied and dbh measured. For all downed material >15 cm

dbh at the time of death, dbh was recorded based on an estimate of breast height measured from the root collar and species was determined based on bark characteristics.

Differences in the percentages of live and dead spruce between the three ecological variants were analyzed using the Kruskal-Wallis single-factor analysis of variance by ranks (Zar 1996, SPSS Inc. 1999). This non-parametric test was used based on previous analyses in Chapter 2, which suggested that any transformation of percent live or dead spruce would not work equally across all three ecological variants. The critical values of Kruskal-Wallis H for small sample sizes were used (Zar 1996). Differences in mean stand age between the three ecological variants were also analyzed using the Kruskal-Wallis test (Zar 1996, SPSS Inc. 1999).

Dendroecological materials and procedures

Increment cores were taken at breast height from each canopy tree because they tend to have less stem decay enabling maximum ring-width series. Cores were then prepared following the standard dendrochronology techniques of Stokes and Smiley (1968). Individual ring-width series were measured to the nearest 0.01 mm using WinDENDRO (Regent Instruments Inc. 2000). For all core samples that had periods of extremely small ring-widths ($\leq$0.5 mm) the ring-width series were measured to the nearest 0.001 mm using the Velmex "TA" System (Velmex, Inc. 1996) in conjunction with MeasureJ2X (2004). Ring-width series were cross-dated using the computer program COFECHA (Holmes 1983) and visual inspected to assist in the detection of measurement and cross-dating errors.

Interpretation of radial growth patterns

Once the ring-width series were dated, ascensions towards the canopy, resulting from overhead canopy mortality, were identified within each series using three radial growth rate criteria (Chapters 3 and 4). First, high rates of early growth (≥1.1, 0.9 and 0.8 mm/year within the dry, mesic and wet, respectively) were used to indicate that a tree was growing in an opening created by disturbance at the time it reached the sampling height (1.3 m). Second, a ≥60 % increase in mean radial growth, when adjacent 15-year groups are compared, was used to identify release from suppression. Previous work (Chapter 3) indicated that this release threshold identified most fine-scale disturbance events that were represented within the data set by release from suppression. The release criterion alone, however, was too liberal, as revealed by the substantial number of release events attributed to regionally synchronous events. In response, a third radial growth rate threshold was developed (Chapter 4) to separate release responses to overhead mortality from regionally synchronous events. The new method assumes that individual standardized ring-width series that diverge from a regional standardized chronology, using the same detrending method, should identify stand dynamics at spatial scales much finer than the individual plot (0.25 ha). In Chapter 2, a cubic-smoothing-spline (50 % frequency response of 50 years) was used to develop species/regionally specific chronologies and to standardize individual canopy trees (Cook and Peters 1981). The regional chronology was subtracted from each standardized series producing a residual ring-width series. One was added to each value of the residual series to avoid negative or erroneously large values when calculating percent divergence over time. Yearly percent divergence values were calculated for each residual series as,

$$[1]\ \%Divergence = \left(\frac{MD_2 - MD_1}{MD_1} \right) * 100$$

where MD_1 and MD_2 equal the preceding and subsequent 15-year residual means, respectively. To be confident that a release event was indeed caused by fine-scale disturbance, and not some other regionally synchronous event (e.g., climate), the release event was only counted if the divergence criterion was met ± five years of the release criterion being met.

Ascensions toward the canopy were then tallied by ecological variant and species. The canopy ascensions, by species within each ecological variant, were correlated with the number of cores sampled of that species within each ecological variant (Zar 1996, SPSS Inc. 1999). The canopy ascensions were then tabulated by ascension type (i.e., gap-origin and release from suppression), species and ecological variant. The relationship between ascension type, species and ecological variant was analyzed using mutual and partial independence tests (Zar 1996).

Disturbance chronologies and frequency

Disturbance chronologies were defined in this study as the percentage of cored trees that ascended towards the canopy during each decade (Frelich and Graumlich 1994, Frelich 2002). Chronologies were constructed for spruce and subalpine-fir separately and then combined to summarize plot level disturbance chronologies. The divergence method truncates the disturbance chronology length because the calculation of residual series begins when the sampling depth of the regional chronology is ≥ five, and the calculation of percent divergence can only begin 15 years thereafter.

Differences in the decadal canopy ascension rates for each species and ecological variant were analyzed by nested ANOVA with species nested within ecological variant (Zar 1996, SPSS Inc. 1999). Explanatory variables in the nested ANOVA were treated as random effects. Past host-specific disturbance events can substantially decrease the relative abundance of one species over others, making it difficult to compare canopy ascension by species. Therefore, decadal ascension rates for each species were standardized by dividing the number of ascensions by the present number of that species sampled within the plot. To assess for temporal variation in the canopy ascension rates between spruce and subalpine fir, two separate nested ANOVA were conducted, including: (1) long-term analysis including the full disturbance chronologies and (2) a short-term analysis including only the last 50 years of each chronology. A 50-year period was selected for the short-term analysis based on empirical data from Chapter 2, which suggests a common stem-reinitiation period for all study plots in the past 50 years.

Point pattern analysis

All living and dead stems ≥15 cm dbh were stem-mapped to assess the univariate spatial pattern within each plot. The function L(d), a transformation of Ripley's K(d), was used to assess the degree to which point patterns deviated from randomness. Ripley's K(d), a second-order statistic, is based on the distances between all pairs of points, counting the number of "neighbours" within a certain distance, d, of each point, with d taking on a range of values. This analysis can be considered an examination of the cumulative frequency distribution of the plant-to-all-plant techniques (Dale 1999).

First, the distance matrix, d_{ij}, between all pairs of points within each plot is tabulated. K(d) is then defined as:

$$[2]\ K(d) = A\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{\delta_{ij}(d)}{n^2}, \text{ with } \delta_{ij}(d) = \begin{matrix} 1 & if & d_{ij} & \leq & d \\ 0 & if & d_{ij} & > & d \end{matrix}$$

Where A is the area of the plot, d is the distance interval considered and n is the number of individuals. Second, to linearize the plot of K(d) against d, as well as to stabilize the variances, L(d) is used to transform K(d) (Diggle 1983):

$$[3]\ L(d) = \sqrt{K(d)/\pi} - d$$

Ripley analysis leads to a graph of L(d) versus the distance d. The expected value of L(d) is zero for trees conforming to a Poisson distribution. Therefore, positive values of L(d) indicate spatial clustering and negative values indicate over-dispersion.

Separate analyses within each plot were completed for live and dead spruce and subalpine fir at one m distance classes up to 25 m using the Ripley module within the program ADS in ADE-4 (Pélissier and Goreaud 1999). Departures from randomness were analyzed by comparing the computed L(d) with a corresponding confidence envelope generated via 1000 Monte Carlo simulations of random patterns at each distance class and then ranked. The 10^{th} and 990^{th} values corresponded to a 0.01 significance level (Diggle 1983).

Spatial-temporal analysis of canopy ascension

The spatial patterns of canopy ascension were used to characterize gap size and the spatial-temporal distribution of fine-scale disturbances within each 0.25-ha plot. This

approach does not require previous knowledge of canopy tree locations. Rather, it assumes that canopy ascension dates coincide with death of canopy trees in the immediate vicinity (Newbery 2001). All spatial-temporal analyses were done using the program RookCase v.0.9.6 (Sawada 1999).

Measures of spatial autocorrelation test whether an observed value at one location is independent of values at neighbouring localities (Sokal and Oden 1978a). In this study, Moran's I was used to test for spatial independence in a canopy ascension date at one location relative to adjacent locations. Each tree can only have one year of ascension towards the canopy in this type of correlation analysis, therefore, only the most recent ascension was used for those trees that showed a response to disturbance in more than one decade (Frelich and Graumlich 1994). Adjacency depends on inter-tree distance and the lag distance set for the analysis (Sokal and Oden 1978a, Sokal and Oden 1978b, Legendre and Fortin 1989, Frelich *et al.* 1993, Frelich and Reich 1995). RookCase v0.9.6 (Sawada 1999) was used to calculate nearest-neighbour distances for each plot. A preliminary ANOVA was used to analyze the nearest-neighbour distances between plots in each ecological variant, and found no significant differences in mean nearest-neighbour distance between trees in each ecological variant ($F = 2.64 < F_{0.05(1),2,12} = 3.89$, $p = 0.112$). Therefore, the grand mean of nearest-neighbour distance was approximately 2.5 m, allowing for spatial analysis at scales $\leq$2.5 m. Therefore, cumulative 2.5-m distance lags (i.e., 0-2.5, 0-5 ..., 0-50 m) were employed. For each distance lag, d, a pair of trees, i and j, were considered neighbours if the distance between them was $\leq$ d. Those not within the distance lag were ignored. The Moran's I coefficients for each distance lag were then calculated as:

$$[4]\ I(d) = \frac{N\sum_i\sum_i w_{ij}(x_i - \bar{x})(x_j - \bar{x})}{W\sum_i (x_i - \bar{x})^2}$$

Where I(d) is the Moran's coefficient for distance lag d, N is the total number of mapped tree locations, x_i (i = 1, ..., N) are the ascension dates at each of the N locations, $w_{ij} = 1$ if points i and j are neighbours within radius d (0 if otherwise), and $W = \sum w_{ii}$ (RookCase v0.9.6 Sawada 1999).

The assumption of randomization was used as the null hypothesis (Upton and Fingleton 1985), whereby the observed dates of canopy ascension are distributed randomly among all locations. Under this hypothesis the Moran's I coefficient is asymptotically normal with a usual range of -1 to 1 and expected value of $E[I(d)] = -(N - 1)^{-1} \approx 0$ (Cliff and Ord 1981). The interpretation of the Moran's I coefficient is similar to interpretations for the standard correlation coefficient (Sokal and Oden 1978a); therefore, the statistic represents the strength of spatial association for canopy ascension dates for each defined distance lag. Values of $I(d) > E[I(d)]$ are considered positively spatially autocorrelated and indicate that canopy ascension dates are similar at distances $\leq$ d. Values of $I(d) < E[I(d)]$ are considered negatively spatially autocorrelated and indicate that canopy ascension dates are dissimilar at distances $\leq$ d.

Significant deviations from the expected value in each distance lag were tested for by calculating the variance of I(d) under the null hypothesis. Standard normal deviates, z(d), were then computed for each distance class as (Duncan and Stewart 1991; RookCase v0.9.6, Sawada 1999):

$$[5]\ z(d) = \frac{I(d) - E[I(d)]}{\sqrt{\text{var}[I(d)]}}$$

Correlograms for each 0.25-ha plot were constructed for both I(d) and z(d) versus d. Significance tests for spatial autocorrelation coefficients for each distance lag, however, do not provide a test of significance for the data set as a whole because the k tests are not independent (Duncan and Stewart 1991). Therefore, significance testing was done first at the global level by determining if at least one p-value for the standard normal deviates was significant at the global level. This was done by using a Bonferroni correction method for multiple tests (e.g. 0.05/k of distance lags (20) = 0.0025) (Sokal and Oden 1978a). If the global test has at least one significant standard normal deviate then the point at which the correlogram becomes non-significant locally ($\alpha = 0.05$) can be interpreted as the average patch size diameter created by disturbance (Frelich *et al.* 1993, Frelich and Reich 1995). When global correlograms included no significant results, the average patch diameter can be interpreted as less than the distance lag.

Results

Non-spatial structure of live and dead trees

The study plots varied considerably within and between each ecological variant. For example, across the three variants the percentage of spruce within the canopy ranged from 10 to 80 % (Table 5.1) and a slight difference was found in the percentages of spruce between the three ecological variants ($\chi^2 = 6.540$, df = 2, p = 0.038). Within ecological variant, $\bar{x}$ ± sd of percent spruce were 48.0 ± 25.1, 34.2 ± 3.7 and 67.6 ± 7.8 % for the dry, mesic and wet

variants, respectively. Subalpine fir, for the most part, made up the remainder of stand composition (Table 5.1).

Across the three ecological variants the densities of trees >15 cm dbh ranged from 308 to 572 trees/ha (Table 5.1), while the within variant density $\bar{x}$ ± sd were 428 ± 120, 405 ± 39, and 398 ± 43 trees/ha for the dry, mesic and wet variants, respectively. The diameter means across all three ecological variants ranged from 26.3 to 35.0 cm (Table 5.1) and the within variant diameter $\bar{x}$ ± sd were 28.7 ± 0.8, 33.0 ± 1.7 and 27.0 ± 0.9 cm for the dry, mesic and wet variants, respectively.

Mean tree age at breast height across all plots ranged from 100 to 150 years (Table 5.1), and there was a significant difference in mean ages between the three ecological variants ($\chi^2 = 8.060$, df = 2, p = 0.018). Within each variant, the $\bar{x}$ ± sd of age at breast height were 131 ± 18, 149 ± 5 and 116 ± 18 years for the dry, mesic and wet variants, respectively.

Across the three ecological variants the percentage of dead spruce ranged widely from 2.5 to 67.7 % (Table 5.2) and there was a significant difference in the percentage of dead spruce between the three ecological variants ($\chi^2 = 9.420$, df = 2, p = 0.009). Within variant $\bar{x}$ ± sd for dead spruce percentages were 39.0 ± 17.9, 43.6 ± 26.0 and 5.4 ± 3.8% for the dry, mesic and wet variants, respectively. A large percentage of the dead tree compositions, up to 47.7 %, were composed of an unidentifiable component (Table 5.2). The within variant $\bar{x}$ ± sd of percent unidentifiable trees were 19.7 ± 17.6, 16.1 ± 10.8 and 40.1 ± 5.5 % for the dry, mesic and wet variants, respectively.

The density of dead trees ranged from 204 to 572 trees/ha across all ecological variants (Table 5.2), while within variant density $\bar{x}$ ± sd were 419 ± 101, 276 ± 50 and 500 ±

44 trees/ha for the dry, mesic and wet variants, respectively. Mean diameters of dead-trees within each plot were quite variable and ranged from 22.8 to 40.5 cm (Table 5.2), while the within variant dead-tree diameter $\bar{x}$ ± sd were 28.7 ± 6.4, 37.2 ± 3.7 and 29.1 ± 2.2 cm for the dry, mesic and wet variants, respectively.

Spatial patterns of live and dead trees

Eleven of the 60 L(d) plots are represented by too few samples (n < 20) for spatial analyses of this kind, however, these plots were retained to illustrate the limitations of point pattern analyses in these forest types at fine spatial scales (Figures 5.1, 5.2, 5.3 and 5.4). Both live spruce and subalpine fir (≥15 cm dbh) show a random spatial pattern at scales <25 m (Figures 5.1 and 5.2). When aggregation of either species did occur, it was variable in magnitude and scale (Figures 5.1 and 5.2). For example, spruce in plots 3, 4 and 5 in the dry variant were aggregated at spatial scales < five m to ≥25 m (Figure 5.1). Dead spruce and subalpine fir trees (≥15 dbh) show random spatial pattern at scales <25 m (Figures 5.3 and 5.4).

Canopy ascension type by ecological variant and species

Of the 491 canopy trees sampled in the dry variant, there were 590 ascensions towards the canopy identified, meaning that present canopy trees often ascend multiple times before reaching the canopy. Within the mesic variant, 721 ascensions towards the canopy were identified in 501 canopy trees and in the wet variant, 495 ascensions towards the canopy were identified within 426 canopy trees (Table 5.3). There was a strong, methodological relationship between the number of cores sampled and the number of

ascensions towards the canopy ($r = 0.886$, $p = 0.003$, $n = 6$). Species, ecological variant and ascension type were not mutually independent (Table 5.4). Furthermore, analyses of partial independencies revealed that species, variant and ascension type were not independent of one another. Therefore, the rejection of the mutual independence indicates a strong interaction between all three variables (Table 5.4).

Disturbance chronologies and canopy ascension by decade

The distributions of decadal canopy ascension percentages were not normally distributed as revealed by a number of the standard deviations being greater than the mean (Table 5.5). To meet the ANOVA assumptions of normality and homogeneity of variance, the data were transformed using the arcsine transformation (Sokal and Rohlf 1995). For the long-term analysis of the full disturbance chronologies, the nested ANOVA found no significant differences in decadal canopy ascension percentages for species nested within variant, or between variants (Table 5.6). For the short-term analysis of the full disturbance chronologies, the nested ANOVA found no significant differences in decadal canopy ascension percentages for species nested within variant, or between variants (Table 5.6). Although the decadal disturbance rates did not differ by variant, mean recruitment into the canopy, based on the full disturbance chronologies, was 7.4, 6.4 and 5.0 % per decade within the dry, mesic and wet variants, respectively (Table 5.5). Many of the plots had decades with no canopy recruitment (Figure 5.5) and maximum decadal canopy recruitment among the three ecological variants were 43.9, 27.5 and 24.7 % per decade for the dry, mesic and wet variants, respectively (Table 5.5).

Spatial-temporal patterns of canopy disturbance

The previous point-pattern analysis suggests that the spatial pattern of canopy trees at scales <25 m is random, indicating the null hypothesis that observed dates of canopy ascension are distributed randomly among all locations is correct. For correlograms with 20 distance lags, the global significance test, using Bonferroni correction, must have at least one Moran's I coefficient with $p \leq 0.0025$. Therefore, the global and local significant levels of z are 1.96 and 2.94, respectively. Few plots in any of the three ecological variants had significant Moran's I coefficients at the global level (Figure 5.6). Plot 3 within the dry variant was globally significant, however, the significant Moran's I coefficients ranged from r-values of 0.029 to 0.060, which suggests weak similarities in ascension dates. A similar pattern occurred for plot 5 within the wet variant where the correlogram was globally significant with r-values only ranging from 0.003 to 0.107 (Figure 5.6). Spatial-temporal aggregation of ascension dates can occur at distances <2.5 m, however, it occurred only once within plot 4 of the wet variant (Figure 5.6). The above results indicate that the average diameter of a canopy gap caused by fine-scale disturbances is approximately equal to the distances between nearest neighbours (≈2.5 m).

Discussion

A central model of plant ecology, the steady-state plant community, has been extensively used to describe the development and maintenance of spruce-subalpine fir forests types throughout the central and northern Rocky Mountains of North America. The steady-state plant community can be defined as the stable endpoint of succession (Clements 1916, Oliver and Larson 1996). Previous interpretations of age- and size-class distributions, and

recruitment and mortality rates, have lead some authors to suggest that spruce and subalpine fir can coexist as a temporally and structurally stable community (Oosting and Reed 1952, Veblen 1986). Other authors have suggested that increasing time between stand-replacing events will inhibit coexistence between these species, and eventually lead to the replacement of spruce by subalpine fir, especially if the two coniferous species are disproportionately abundant within the understory and have similar mortality rates (Day 1972, Peet 1981, Newbery 2001). Within the central interior of British Columbia both species are relatively long lived, often approaching and exceeding 200 years of age. Therefore, it is not surprising that the two species coexist to some extent within late successional stages of forest development (Chapter 2, Figure 2.2). Observations made within this study, together with previous work in British Columbia, have identified a range of variation in the age, size, spatial structure and recruitment rates of trees in old spruce-subalpine fir forests (Kneeshaw and Burton 1997, Lewis and Lindgren 1999, Parish *et al.* 1999a, Parish *et al.* 1999b, Antos and Parish 2002a, Antos and Parish 2002b). The results of this study suggest that stand dynamics in mature spruce-subalpine fir forests of central British Columbia are not necessarily described properly by the steady-state community concept, but are more a product of punctuated disturbance events acting at multiple spatial and temporal scales. This is consistent with the findings of Parish *et al.* (1999b) where the composition of a mature spruce-subalpine fir forest in southeastern British Columbia was the result of multiple scales of disturbance of differing intensities, together with recruitment during interdisturbance periods. Fine-scale disturbance events may bring about continuous stand-level maintenance and renewal over extended periods of time in the absence of intermediate- to coarse-scale disturbance events; however, empirical data presented within this study and previous work

(Chapter 2) suggest that change in species composition tend to be abrupt and due to intermediate- and coarse-scale disturbance events.

The accuracy of historical reconstruction is greatly affected by the overlap between disturbance types of varying spatial and temporal scales. Lorimer and Frelich (1989) and Frelich and Graumlich (1994) point out that recent disturbances can remove members of an older cohort, replacing them with younger cohorts. Therefore, the potential for one species to ascend towards the canopy over another is not always discernable. Within plots 1 and 2 of the dry variant, subalpine fir was consistently the most frequent species releasing and ascending towards the canopy (Table 5.3). Within plots 3, 4 and 5 of the dry variant, the most recent coarse-scale disturbance event in the latter part of the 1800s, which caused 43.9% of the sample trees to ascend towards the canopy (Table 5.5), allowed spruce to establish and dominate over subalpine fir (Figure 5.5). In regions where fire acts largely as a stand-replacing disturbance agent that allows few, if any, trees to survive, spruce and/or pine tends to dominate seedling establishment (Veblen *et al.* 1991). The total number of spruce entering the canopy, and the large proportion of gap-origin events compared to the small proportion of release events, supports this (Table 5.3). Within the mesic variant, subalpine fir was consistently the most frequent species releasing and ascending towards the canopy (Table 5.3). Within the wet variant, western balsam bark beetle during the 1920s and 30s substantially reduced the proportion of subalpine fir (Chapter 2, Figure 2.4). In response, spruce was the most frequent species ascending into the canopy (Table 5.3). This refutes evidence that increasing periods of time between stand-replacing events will eventually lead to the replacement of spruce by subalpine fir.

If the number of canopy ascensions is related to new disturbances that remove members of an older cohort, then ascensions alone are insufficient to provide insight for the

potential of one species to ascend into the canopy over another. Although it has been suggested that increasing periods of time between stand-replacing events will lead to the eventual replacement of spruce by subalpine fir, there is little evidence in any of our plots that suggests this is actually occurring as a result of fine-scale disturbance. Neither the long-term nor the short-term analyses support the idea of replacement, given that the decadal canopy disturbance rates for species nested within ecological variant did not differ (Table 5.6).

The mean decadal canopy disturbance rates of 7.4, 6.4 and 5.0 % within the dry, mesic and wet variant plots, respectively, suggest that fine-scale disturbance events do gradually maintain and renew the current forest structure in the absence of intermediate- or coarse-scale disturbance events. Although the differences between the ecological variants were not statistically significant, the lack of significance could be explained by lack of statistical power, which can be attributed to the high variation in the estimates of canopy disturbance frequencies within the dry variant (Table 5.5). Within the dry variant, the mean and maximum decadal disturbance rates were 7.4 and 43.9 %, respectively. This relatively higher rate of disturbance can be explained by the intermediate- and coarse-scale disturbance events that we were unable to partition completely from fine-scale events. The stand-level rates of fine-scale canopy disturbance in the absence of stand-replacing events tend to decrease, from the dry-warm interior plateau to the wet-cold foothills of the Canadian Rockies (Table 5.5).

The estimates of decadal canopy disturbance rates are consistent with previous estimates of canopy disturbance rates. Within spruce-subalpine fir forests of the mesic variant, located less than 100 km south of the mesic variant plots in this study, Newbery (2001) estimated canopy disturbance rates ranging from 5 to 8 % per decade. Within the

northern hardwood forests of Upper Michigan, Lorimer and Frelich (1989) estimated canopy disturbance rates ranging from 5.7 to 6.9 % per decade. Within the hemlock-hardwood forests of Upper Michigan, Frelich and Graumlich (1994) estimated canopy disturbance rates ranging from 2 to 12 % per decade. Runkle (1985) points out that the rates of forest disturbance average ≈10 % per decade and range ≈ five to 20 % per decade, with little variation between forest types, despite wide differences in vegetation and agents of disturbance. The methods within our study were specifically designed to partition the majority of the intermediate- and coarse-scale disturbance events from fine-scale events. The end goal was to describe the fine-scale disturbance regimes. Therefore, it is not surprising that the canopy disturbance rates in this study are at the low end of the range of disturbance rates outlined by Runkle (1985), as his values describe all disturbance types combined. Disturbance rates for specific agents of disturbance, or for particular components of a disturbance regime, are expected to be relatively low (Runkle 1985).

A decreasing rate of fine-scale disturbance from the driest to wettest ecosystems, at first, seems counterintuitive. Preliminary etiological analyses conducted for the three ecosystems within this study, suggest that from the dry to wet variant, a number of fine-scale disturbance agents tend to decrease in abundance, and some agents become completely absent (R.D. Thompson, UNBC, unpublished data). For example, the incidence of *Inonotus tomentosus* (Fr.) Teng., the causal agent of tomentosus root disease, is greatest and most variable within the dry variant. Within the mesic variant, incidence of this disturbance agent decreases, and within the wet variant, it is completely absent. Lewis *et al.* (2004) found that incidence of tomentosus root disease was negatively correlated with direct measurements of soil moisture. Whitney (1976) also found that disease incidence varied inversely with soil moisture regimes as determined indirectly using a classification system. The relative soil

moisture content of zonal sites selected within the wet variant are greater than the soil moisture content of zonal sites within the dry variant (Meidinger and Pojar, 1991), and may partially explain the declining incidence of this disturbance agent. From dry to wet ecosystems, the climate may become inhospitable to some agents of disturbance. If Runkle's (1985) hypothesis – rates of disturbance for specific agents of disturbance will be less than estimates for an entire regional disturbance regime – is correct, then a decrease in the number of different fine-scale disturbance agents from the dry-warm interior plateau to the wet-cold foothills of the Canadian Rockies may partially explain the decreasing rates of stand-level fine-scale disturbance.

Within this study, point-pattern analysis of live and dead spruce and subalpine fir stems (≥15 dbh) resulted in random spatial patterns at scales <25 m across all ecological variants. Parish *et al.* (1999b) found that mortality was random within canopies of subalpine, spruce-subalpine fir forest types, which in turn leads to random patterns of release. Based on our Moran's analysis, canopy ascension dates were spatio-temporally random, and average canopy openings were ≈2.5 m in diameter across all ecological variants. Canopy opening diameters, however, varied enormously from small (<2.5 m diameter) to fairly large (27.5 m within the dry variant and >50 m within the wet variant) openings created within the canopy (Figure 5.6). The random spatial pattern of canopy ascension could be due to the etiology of the fine- and intermediate-scale disturbance agents occurring within these forest types, which are primarily biotic, and may not result in gap-contagion. These results are similar to those of Newbery (2001), who found that gap sizes averaged less than seven m in diameter, but varied from small (<7 m) to large (≈28 m diameter) canopy openings within sites similar to our mesic variant plots. Frelich and Graumlich (1994) found a lack of spatial autocorrelation of tree ascension dates for the smallest lag distance defined (10 m). This meant that the

average canopy opening diameter was less than 10 m within the hemlock-hardwood forests of Upper Michigan. The difference in average canopy opening diameter between our research and the results of Newbery (2001) and Frelich and Graumlich (1994) can be explained by the lag distance specified in the spatial autocorrelation analyses (2.5 m versus 7 m, respectively) and how samples are collected for the Moran's I analyses. The results of Newbery (2001) and Frelich and Graumlich (1994) were based on the spatial analysis of ascension dates sampled from evenly spaced grid points (7 and 10 m, respectively). The estimates of canopy opening size, within the present study, were based on an irregular lattice of stem-mapped points. This allowed spatial analysis at nearest neighbour distances (2.5 m) which is much smaller than previous work. The results suggest that canopy openings on average tend to be small, spatially independent and caused by the death of single trees.

Due to the variability in the distribution of canopy opening size, however, a number of disturbance processes are working together through time. First, the relatively random spatio-temporal pattern of small openings is indicative of structures resulting from a suite of fine-scale disturbance agents. Second, the larger patch structures, identified through point-pattern analyses, are more likely indicative of the wide-spread insect outbreaks that were suggested in Chapter 2. Together, this provides further evidence for the overlap between different types of disturbances of differing intensities, together with fine-scale recruitment between intermediate-scale disturbance events.

In conclusion, the results of this study suggest that intermediate-scale disturbance events have played a larger mediating role over distinct changes in stand structure than that of fine-scale disturbance events. Further, this study supports the proposal of Wilson and Agnew (1992) that the punctuated equilibrium concept be extended to the spatial and temporal processes in plant ecology. Frelich and Graumlich (1994) suggest that for this

concept to work within a forest ecology framework, a landscape of given size must exist in a state of "punctuated quasi equilibrium" whereby disturbances with fine spatial extent relative to the landscape maintain a quasi equilibrium during the intervals between larger disturbances with a longer rotation period that punctuate the more stable periods. As we move across the central interior of British Columbia, regardless of the climatic gradient, examples of nested disturbance types are undoubtedly responsible for the patterns we see today on the landscape. Therefore, it is feasible to extend this concept to even finer spatial scales such as the individual stand composed of spruce and subalpine fir. To have a disturbance regime of hierarchically nested disturbance types on a given forest landscape, catastrophic disturbances such as stand-replacing fire must occur rarely so that several tree generations may pass between disturbances. The consideration of disturbance events at multiple scales shows that fine-scale disturbance exhibits continuous stand level maintenance and renewal; furthermore, that changes in stand composition can be multidirectional and tend to be abrupt, due to intermediate-scale disturbances such as those caused by insect outbreaks.

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Table 5.1. Structural attributes of the canopy layer (live trees ≥15 cm diameter at breast height, dbh).

Variant	**Dry**					**Mesic**					**Wet**				
Plot	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Approx. stand initiation	1760	1760	1840	1840	1800	1740	1760	1700	1750	1760	<1650	<1650	<1650	<1650	<1650
Stand Density (trees/ha)	344	308	540	572	376	364	400	448	372	444	432	412	356	352	440
Stand Composition (%)															
Spruce	35	10	70	66	59	35	30	38	38	31	60	65	80	70	63
Subalpine fir	64	90	21	15	37	60	70	63	61	69	40	33	19	30	37
Other	1	0	9	19[a]	4	4	0	0	1	0	0	2	1	0	0
Stand structure															
dbh (cm, mean)	30.8	29.2	29.4	28.7	30.2	35.0	31.6	34.3	31.0	33.0	26.4	26.8	27.3	26.3	28.4
dbh (cm, s.d.)	13.2	10.4	11.3	9.6	10.7	13.4	13.2	14.9	13.1	14.2	11.1	11.9	12.3	12.2	13.9
Age (mean)	151.0	150.7	114.1	122.6	117.4	152.7	139.8	151.6	151.0	151.4	103.0	105.3	147.2	109.2	119.3
Age (s.d.)	50.3	43.0	33.1	29.1	18.6	54.4	56.6	59.0	67.3	58.9	59.1	49.1	72.4	46.1	56.4

[a] Plot 4 within the dry variant, due to the random nature of all plot locations, had a small patch of *Pinus contorta* located on the plot boundary.

Table 5.2. Structural attributes of dead trees ≥15 cm diameter at breast height (dbh).

Variant	**Dry**					**Mesic**					**Wet**				
Plot	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Density (trees/ha)	428	572	356	304	436	336	260	204	312	272	452	568	516	480	488
Composition (%)															
Spruce	15	29	58	54	39	12	68	47	37	54	4	3	12	3	7
Subalpine fir	51	27	28	24	47	61	29	43	35	29	49	63	44	60	57
Other	1	0	9	14	5	1	2	0	1	0	0	0	0	0	0
Unidentifiable	33	44	4	8	9	26	2	10	27	16	48	35	44	38	37
Structural attributes															
dbh (cm, mean)	35.4	35.7	22.8	23.5	26.2	32.9	39.6	33.4	39.6	40.5	32.2	28.1	26.5	28.5	30.0
dbh (cm, s.d.)	12.6	13.6	7.1	9.7	10.9	11.5	12.0	11.9	15.1	15.5	9.7	7.8	9.7	8.9	10.1

Table 5.3. Proportion of canopy ascension types grouped by variant and by species.

Variant	Species	Number of core samples	Total number of ascensions	Type of ascension (proportion of total)	
				Release	Gap origin
Dry	**Spruce**	282	337	0.36	0.64
	Subalpine fir	209	253	0.52	0.48
	Pooled	**491**	**590**	**0.43**	**0.57**
Mesic	**Spruce**	173	297	0.59	0.41
	Subalpine fir	328	424	0.63	0.37
	Pooled	**501**	**721**	**0.62**	**0.38**
Wet	**Spruce**	334	294	0.28	0.72
	Subalpine fir	161	132	0.30	0.70
	Pooled	**495**	**426**	**0.29**	**0.71**

Table 5.4. Summary statistics of mutual and partial independence tests between species, variant and ascension type using contingency analyses. Column 1 represents the variable(s) being tested for independence. Column 2 represents the variables against which column 1 is tested against in the case of partial independence.

Independence test	**Test grouping**		χ^2	**df**	*p*
	Column 1	**Column 2**			
Mutual	Species Variant Ascension		245.2	7	<0.001
Partial	Species	Variant Ascension	105.5	6	<0.001
Partial	Variant	Species Ascension	188.4	6	<0.001
Partial	Ascension	Species Variant	140.7	5	<0.001

Table 5.5. Summary statistics for the untransformed decadal percentages of canopy ascension grouped by variant and species.

Variant	Species	Mean (%)	Standard deviation	Maximum (%)
Dry	Spruce	7.8	10.6	47.3
	Subalpine fir	7.2	9.6	46.4
	Pooled	7.4	8.7	43.9
Mesic	Spruce	7.5	7.2	31.3
	Subalpine fir	5.9	6.2	28.6
	Pooled	6.4	5.4	27.5
Wet	Spruce	5.1	5.7	24.6
	Subalpine fir	4.8	6.7	32.4
	Pooled	5.0	5.4	24.7

Table 5.6. Nested ANOVA results of percent decadal canopy ascension over the long-term and the short-term (i.e., last 50 years of each disturbance chronology).

Test	Source	SS	df	MS	F	p
Long-term	**Variant**	805.665	2	402.833	4.761	0.117
	Species (Variant)	253.835	3	84.612	0.947	0.418
	Error	47527.119	532	89.337		
Short-term	**Variant**	501.215	2	250.608	1.952	0.286
	Species (Variant)	385.211	3	128.404	1.331	0.267
	Error	13753.120	144	96.508		

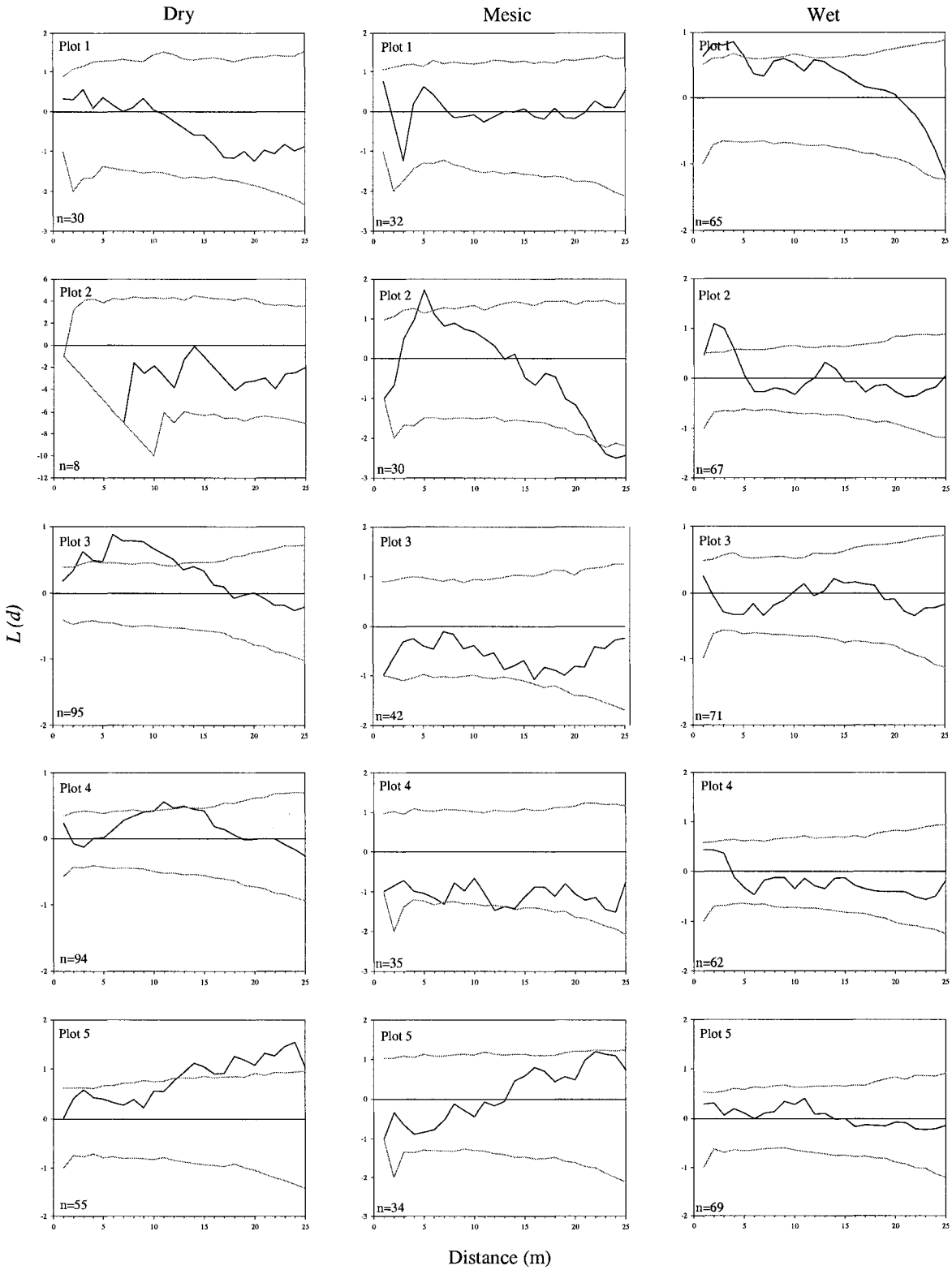

Figure 5.1. Graph of L(d) versus distance for live spruce ≥15 cm DBH. The solid line shows L(d), and the dotted grey lines show the 99% confidence envelope for random distribution. Positive values of L(d) indicate clustering. Plots are grouped as dry (left), mesic (middle) and wet (right) variants.

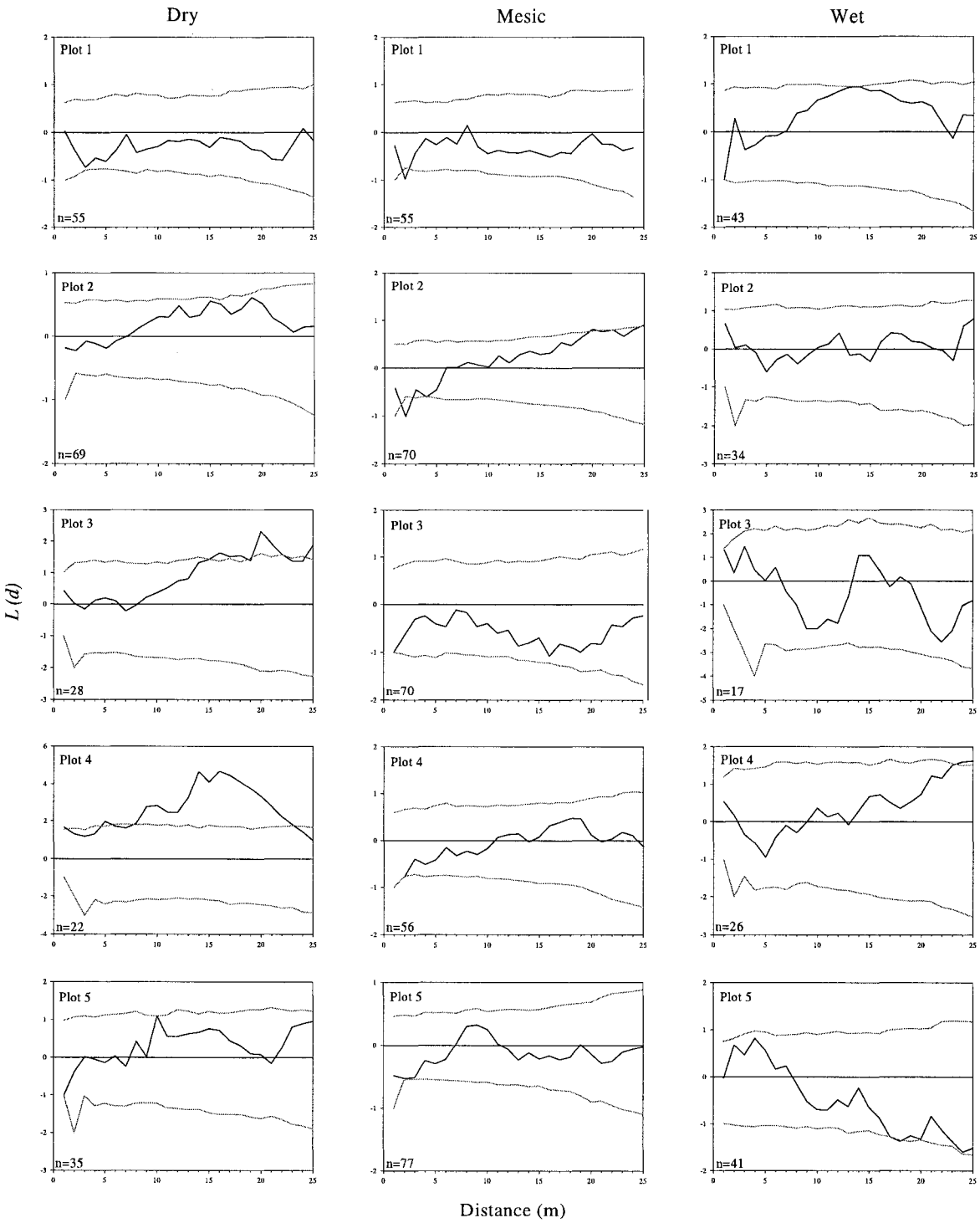

Figure 5.2. Graph of L(d) versus distance for live subalpine fir ≥15 cm DBH. The solid line shows L(d), and the dotted grey lines show the 99% confidence envelope for random distribution. Positive values of L(d) indicate clustering. Plots are grouped as dry (left), mesic (middle) and wet (right) variants.

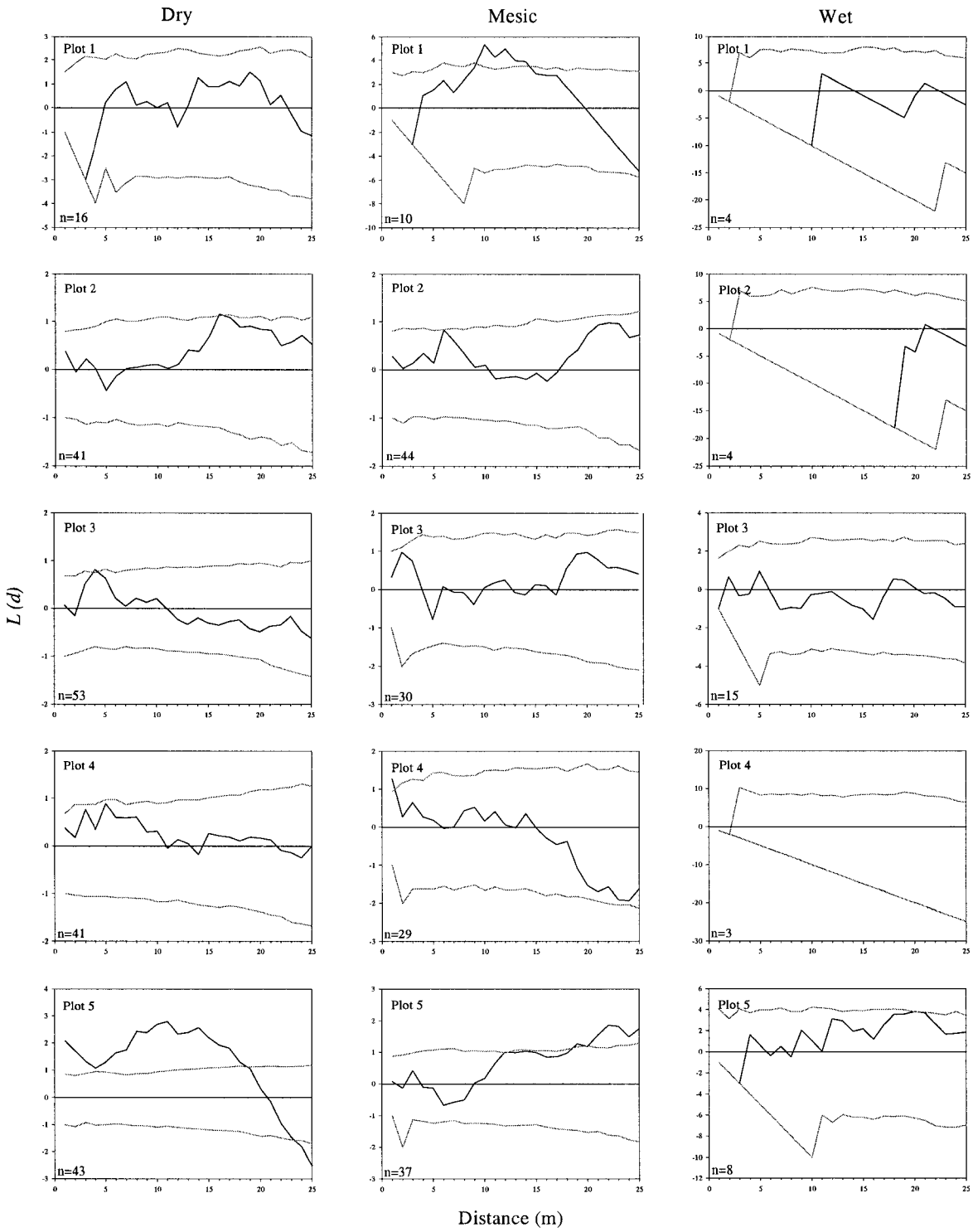

Figure 5.3. Graph of L(d) versus distance for dead spruce ≥15 cm DBH. The solid line shows L(d), and the dotted grey lines show the 99% confidence envelope for random distribution. Positive values of L(d) indicate clustering. Plots are grouped as dry (left), mesic (middle) and wet (right) variants.

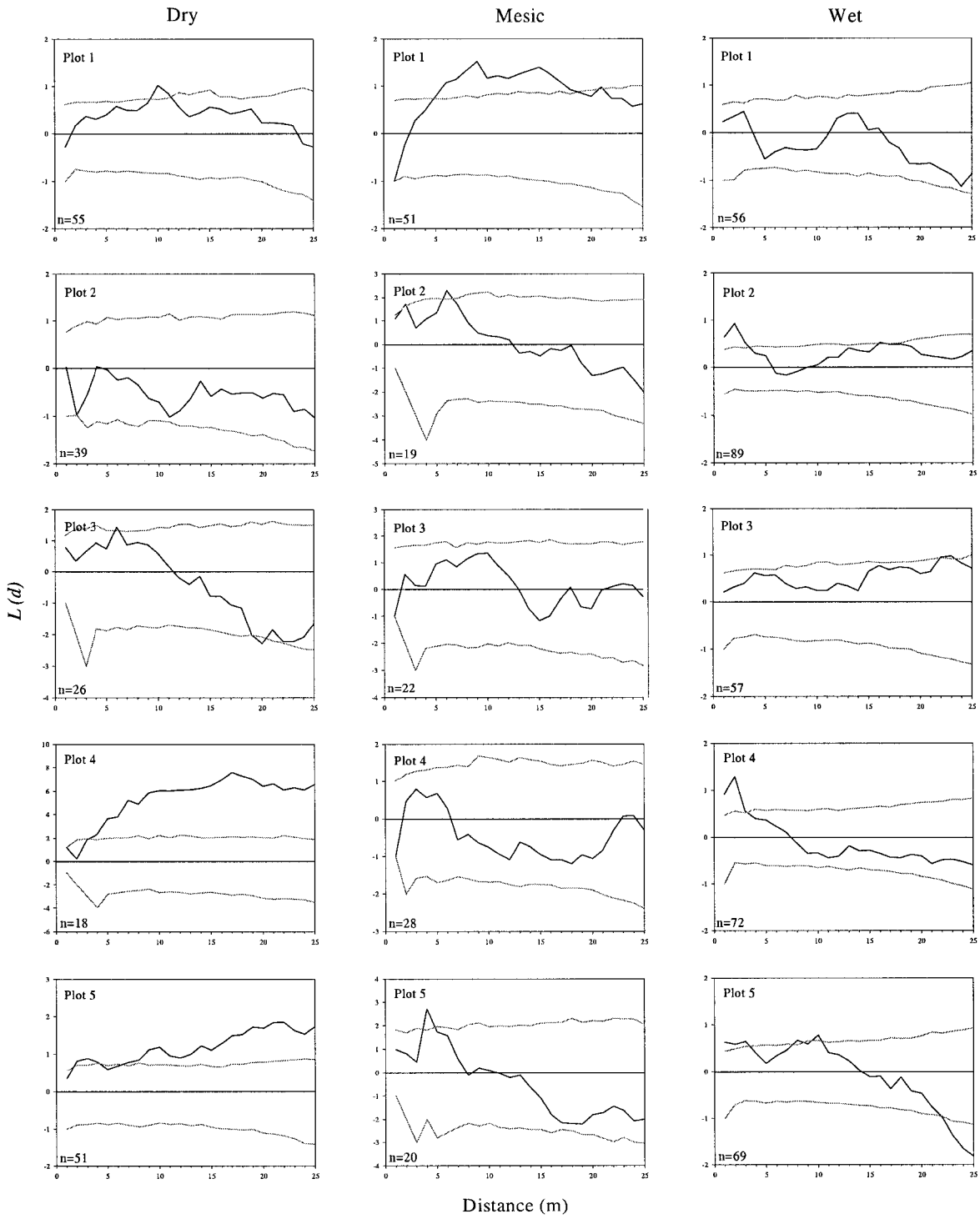

Figure 5.4. Graph of L(d) versus distance for dead subalpine fir ≥15 cm DBH. The solid line shows L(d), and the dotted grey lines show the 99% confidence envelope for random distribution. Positive values of L(d) indicate clustering. Plots are grouped as dry (left), mesic (middle) and wet (right) variants.

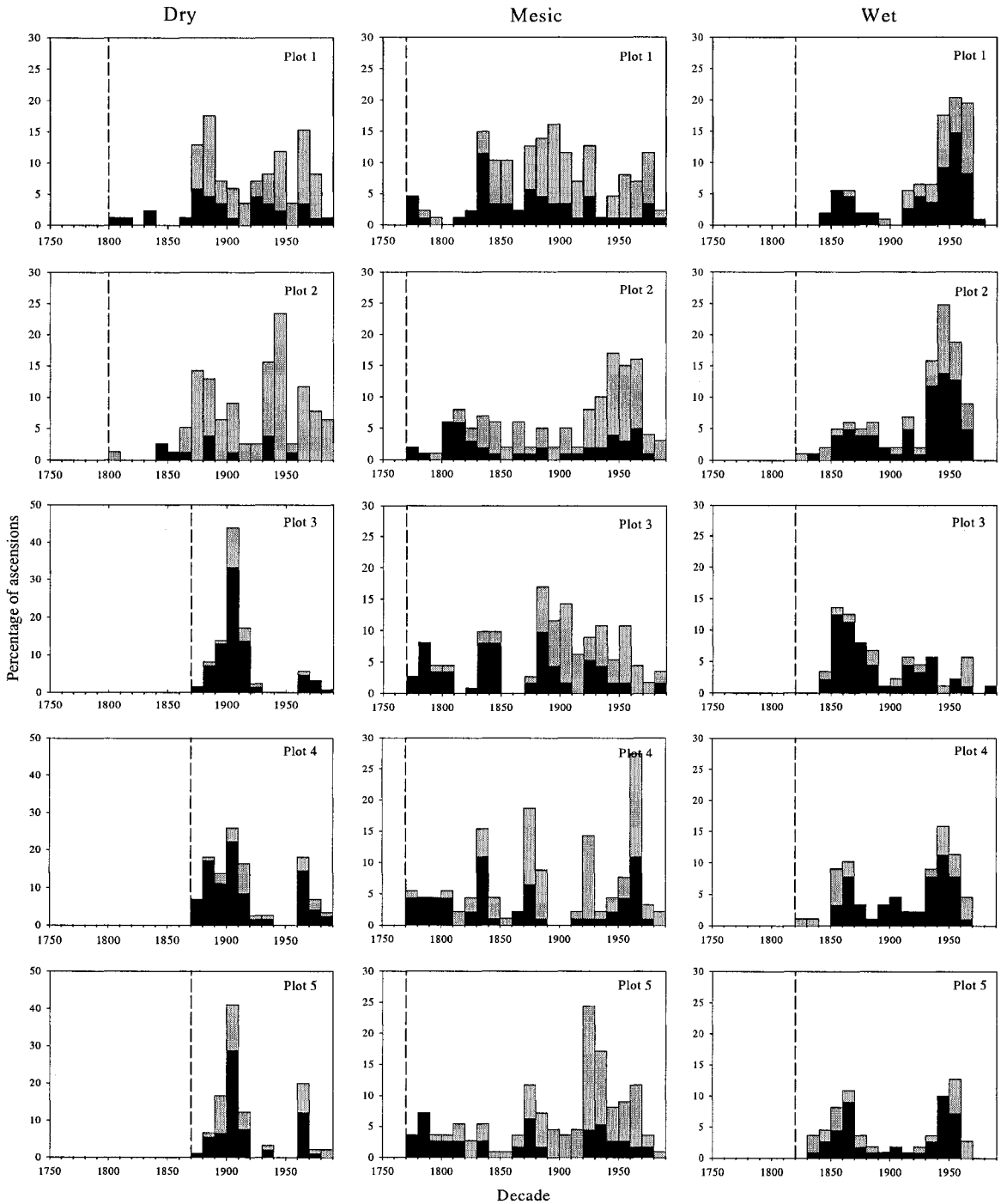

Figure 5.5. Disturbance chronologies for each plot showing the percentage of cored trees ascending to the canopy in each decade. Each graph represents one plot with the plot identification at top right. Black and grey bars represent spruce and subalpine fir, respectively. Vertical dashed lines indicate chronology length. Plots are grouped as dry (left), mesic (middle) and wet (right) variants.

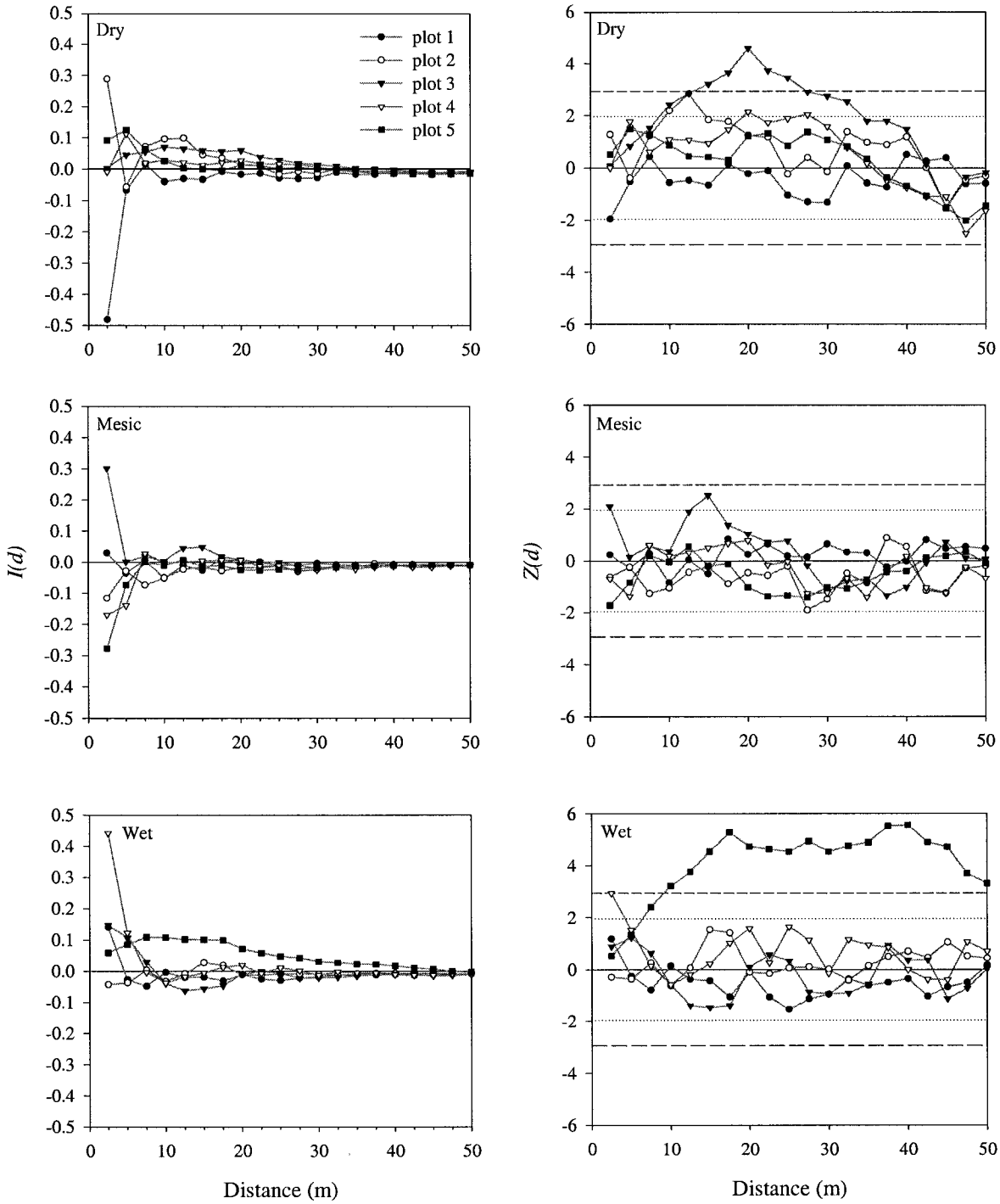

Figure 5.6. Correlograms of the Moran's I coefficients (left) and standard normal deviates (right) for canopy ascension dates by distance lag. Horizontal long and short-dashed lines (right) represent the global and local significance levels, respectively.

CHAPTER 6 – SYNOPSIS: SUMMARY OF FINDINGS, MANAGEMENT IMPLICATIONS, FUTURE RESEARCH AND CONCLUSIONS

Disturbance in forested ecosystems

Natural disturbance ecology encapsulates the interrelationships between the biotic and abiotic components of an ecosystem, attempting to characterize the patterns and processes influencing mortality and regeneration. In most forested ecosystems, disturbance is a key driver of ecosystem function, affecting landscape pattern (DeLong and Tanner 1996, Hawkes *et al.* 1997, DeLong 1998), stand structure (Oliver and Larson 1996, Kneeshaw and Burton 1997, Lewis and Lindgren 1999) and biodiversity (Bunnell 1995).

White and Pickett (1985) proposed the most widely used definition of disturbance as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. As part of their definition, disturbances are regarded as discrete events in time. I suggest, however, that it is their persistence on the landscape that sustains the patterns and processes so important in maintaining biodiversity. Therefore, stand- or landscape-level disturbances are not only characterized by their spatial structure, but include the temporal patterns of mortality for the dominant individuals over extended periods of time. Collectively, the various spatial and temporal components are referred to as a plant community's "disturbance regime" (Runkle 1985).

Historically, the disturbance regime has been defined in terms of the major catastrophic events that originate from the physical environment, and was regarded as an exogenous agent of vegetation change (White 1979). This paradigm has lead to a strong research and management focus on catastrophic wildfire as the dominant agent of disturbance

within boreal ecosystems of Canada. These ecosystems generally have short fire return intervals that maintain the landscape with low diversity in age-class structure, simply because fire return intervals are shorter than tree life spans (Veblen 1986; Frelich and Reich 1995). As the coarse-scale stand dynamics of sub-boreal ecosystems are similar to boreal ecosystems, a focus on stand-replacing fire has been adopted for the sub-boreal and, in many cases, the subalpine ecosystems of central British Columbia. Although this focus has been informative, an understanding of what occurs in the natural absence of fire is limited.

In order to contribute to the knowledge and understanding of forest dynamics during the intervals between stand replacing events, I have attempted to quantify and characterize fine-scale disturbance as it varies within and between three distinct sub-boreal and subalpine ecosystems of central British Columbia. The specific research questions were:

1. What are the spatial and temporal patterns of fine-scale disturbance across three climatically distinct, mature spruce-subalpine fir forest types and do they differ;
2. What role has the combined effects of fine-scale disturbance played in forging the present forest composition and structure; and
3. Does fine-scale disturbance lead to considerable changes in future forest composition?

The remainder of this chapter summarizes the findings of this research, discusses potential forest management applications and discusses future research needs.

Ecological summary

Disturbance histories

Mortality of canopy trees was indicated indirectly through canopy ascension information as far back as 1700 within the SBSdw3, SBSwk1 and ESSFwk2 variants. The

oldest individuals in these stands were over 290 years in the SBSdw3 variant, well over 300 in the SBSwk1 variant and approaching 400 years of age in the ESSFwk2 variant, indirectly suggesting that stand-replacing events can remain absent from these stands for extensive periods of time. In the absence of stand-replacing events, a number of disturbance agents have acted to modify stand structure. In the mesic variant plots and in the oldest plots (1 and 2) of the dry variant, canopy mortality during the 1870s removed substantial proportions of the spruce basal area, which provided opportunity for canopy ascension. Within the ESSFwk2 variant there were two disturbance events. The first occurred in the 1830s, probably spruce beetle, and the second in the early 1930s has been identified as western balsam bark beetle. These periods were present within all ESSFwk2 variant plots and represent regionally synchronous outbreaks. The 1930s outbreak of western balsam bark beetle removed a substantial proportion of subalpine fir, which released both spruce and subalpine fir.

Canopy disturbance rates

The average canopy disturbance rates were 7.4, 6.4 and 5.0 % per decade within the SBSdw3, SBSwk1and ESSFwk2 variants, respectively. These disturbance rates were developed based on the species pooled because there were no significant differences between the canopy disturbance rates for spruce and subalpine fir. From the driest to the wettest variants, two changes occurred with regard to the fine-scale component of their respective disturbance regimes. First, maximum decadal canopy disturbance rates decreased and second, variation in the disturbance rates decreased.

Canopy opening size

Canopy opening diameter averaged ≈2.5 m, corresponding to a gap area of ≈ five m^2. Note that this gap size estimate was limited to the lag distance specified for the spatial analysis (2.5 m), corresponding to the nearest-neighbour distances measured across all three ecological variants. Larger gaps, as a result of multiple tree mortalities, were present in all ecological variants; however, these events occurred less frequently than single tree gaps. Furthermore, results from the point pattern and spatial-temporal analyses do not imply strictly that the single tree mortalities – causing average sized canopy openings – are independent events randomly dispersed through time. Lewis and Lindgren (2000), in their conceptual model of disturbance ecology within sub-boreal and subalpine ecosystems, suggest that decay fungi are important agents of disturbance, modifying the forest matrix by causing individual or group mortalities over extended periods of time. Normally, decay fungi do weaken the roots and/or the bole to such an extent that breakage is inevitable. Wind storms, however, can aggregate such breakage in time, resulting in many small, spatially distinct openings in the forest matrix that appear as a single event. The spatial pattern analysis of dead stems supports this because the co-ordinates were generally random in nature and spatial contagion rarely occurred. It was also found that regionally synchronous bark beetle outbreaks cause similar spatial-temporal patterns throughout the forest matrix: however, mortality is host specific and the disturbance event extended over larger spatial areas.

Stand composition, canopy replacement and future stand composition

The results of this study indicate that increasing periods of time between stand-replacing events do not necessarily lead to the replacement of spruce by subalpine fir. In

many plots, subalpine fir was exceedingly abundant in smaller diameter classes and younger breast height age classes, suggesting that subalpine fir would eventually displace spruce. Size and age distributions, however, are static representations of stand dynamics. Due to the relatively shorter fire-return intervals within increasingly dry/warm ecosystems, shifting much of the landscape back successionally, the species shift from spruce to subalpine fir is observed more often than not. Furthermore, the abundance in subalpine fir was rarely due to a slow and methodical replacement of spruce caused by fine-scale disturbance. The complete opposite occurred within the ESSFwk2 variant during the 1930s western balsam bark beetle outbreak that substantially reduced the proportion of subalpine fir within all ESSFwk2 variant plots. These results suggest a common theme across all mature, spruce-subalpine fir forest types found within the central interior of British Columbia. That is, future canopy composition is not unidirectional or convergent, always leading to subalpine fir. On the contrary, forest composition is quite dependent on the "punctuated" disturbance types discussed in Chapter 5. That is, individual stands can exist in a state of "punctuated quasi equilibrium" whereby relatively small-scale disturbances will maintain and renew forest structure during the intervals between intermediate- scale disturbances with a longer rotation period that punctuate the more stable periods.

Management implications

It has been suggested that successful conservation and maintenance of overall forest health will require an understanding of disturbance patterns and processes (Pickett and Thompson 1978, White 1979, White and Pickett 1985, Bergeron *et al.* 1999, Lewis and Lindgren 2000). It has also been suggested that ecological values inherent in forest

ecosystems can best be maintained by using forest practices that mimic natural disturbance regimes (Bunnell 1995, Hawkes *et al.* 1997, Bergeron *et al.* 1999).

The disturbance chronologies presented in this research indicated that decadal canopy disturbance was 7.4, 6.0 and 5.0 % within the SBSdw3, SBSwk1 and ESSFwk2 variants, respectively. In that order, this would correspond to approximately 22 to 42, 22 to 33 and 18 to 22 mortalities per hectare per decade based on the current tree densities in each ecological variant. Furthermore, again in that order, the average plot diameters of dead canopy trees ranged from 22 to 38, 33 to 41 and 27 to 32 cm dbh. Species composition of dead trees (≥15 cm dbh) within the SBSdw3, SBSwk1 and ESSFwk2 variants ranged anywhere from 15 to 58, 12 to 68 and four to 12 % spruce, respectively.

To achieve the above ranges, partial-cut systems conducted every 10 years, would remove an extremely wide range of possible densities, diameters and portions of each constituent species (e.g., percent spruce). Furthermore, harvests would take on a variety of canopy opening sizes, with the average diameter ≈2.5 m. This suggests that a collection of single tree and small group selection systems would be the most appropriate to maintain natural forest structure. Unlike "beetle proofing" a stand to minimize the future chance of economic loss due to bark beetle infestations, these partial cuts would create uncertainty around future intermediate-scale disturbance events. Beetle proofing is the application of silvicultural treatments (e.g., stand thinning) meant to promote resistance in the remaining trees to future beetle outbreaks and to minimize economic loss. Partial cut systems do not minimize additional mortality due to the continuous low intensity nature of fine-scale disturbance. As a result, there is an additive effect, where the expected fine-scale disturbance events continue through time in addition to the removal of stems during each partial cut. Therefore, it is unclear whether or not the spatial and/or temporal patterns of fine-scale

disturbance, as described in this thesis, can be mimicked reasonably by the application of partial cut silvicultural systems.

An alternative approach is to focus on the imitation of intermediate-scale disturbance events, such as the insect outbreaks identified within this study. For example, within the watershed where the ESSFwk2 variant plots were sampled, three mortality events show up in the majority of the mature tree ring records in the 1710s, 1830s and 1930s, suggesting that the events are at least synchronous within the watershed. Although not conclusive, because of our short dendroecological record, let us assume that these events were caused by spruce beetle and western balsam bark beetle, and the approximate return-interval would be 200 years with a 100-year lag between bark beetle species.

The application of this disturbance regime in the appropriate ecosystem would involve harvest of one species (e.g., spruce), from a moderately narrow group of diameter classes based on host susceptibility, over a 10-year period. This does not mean removing all of the trees from one large, economically valuable, diameter class (i.e., high-grading). The proportion removed from the susceptible diameter classes would be aligned with the proportions historically removed by the disturbance agent (e.g., ≈35 % of spruce stems >45 cm and ≤65 cm dbh). Regeneration would focus on the alternative species (e.g., subalpine fir). The area would then be left unharvested until the end of the 100-year period, when the process would begin again, although the focus would shift to the removal of subalpine fir and the regeneration of spruce. Essentially, this silvicultural practice would be thinning from above and would place small, spatially random, openings into the forest matrix over coarse spatial scales.

In contrast to the application of partial cutting silvicultural systems, which involves an entry every 10 years in any given area and requires continual activity over an entire

management area such as an entire watershed, imitating the temporal interchange between spruce beetle and western balsam bark beetle over a 200 year rotation period would only require one 10-year entry every 100 years.

Much like bark beetle proofing stands to minimize the future chance of economic loss due to bark beetle infestations, this alternative silvicultural system would minimize the chance for future intermediate-scale disturbance events. Conversely, such a silvicultural system would not minimize further mortality due to the continuous low intensity nature of fine-scale disturbance within any given stand of trees. Therefore, the continuous long-term inputs of such things as wildlife trees and coarse woody debris would be maintained as a result.

DeLong (2002) has developed a Natural Disturbance Unit (NDU) model for the entire Prince George Region. In comparison to British Columbia's five natural disturbance types (Ministry of Forests British Columbia 1995), for the Prince George region alone there are nine NDU. The SBSdw3 variant plots fall within the Moist Interior-Plateau NDU with fire and mountain pine beetle (*Dendroctonus ponderosae*) as the key stand-replacement disturbance agents (DeLong 2002). The disturbance cycle assigned to this NDU is 100 years based on work by Andison (1996) and DeLong (1998). The SBSwk1 variant plots fall within the McGregor Plateau NDU with fire as the key stand-replacement disturbance agent (DeLong 2002). The stand replacement disturbance cycle assigned to this unit is 220 years. The ESSFwk2 variant plots fall within Wet Mountain NDU with stand-replacement disturbance events occurring at irregular intervals with as much as 1000 years between such events on any site (DeLong 2002).

Confronting forest ecosystem management are other management philosophies and approaches such as integrated resources management, conservation, and zoning. Within the

wet mountain NDU, typical old forest characteristics historically dominated the landscape. Therefore, it seems reasonable to apply the alternative silvicultural approach that attempts to mimic bark beetle outbreaks over large spatial areas. In contrast, the disturbance cycle within the SBSdw3 is 100 years. Therefore, very little connectively exist between the rarely occurring mature spruce-subalpine fir forest types. Few ecological benefits would therefore be realized by micro-managing old remnant patches that would be left behind naturally by wildfire. Delong (2002) suggests that maintaining mature forest patches could be accomplished by rotating old forest reserves. Within the McGregor Plateau NDU, old forest characteristics were historically dispersed unevenly across the landscape (i.e., rare in some areas and abundant in others). It seems reasonable to apply some combination of the two extremes discussed above. Therefore, in some watersheds, silvicultural systems that attempt to mimic the complex interchange between fine- and intermediate-scale disturbance events could be used. In other watersheds, larger patches with reserves could be used to mimic catastrophic wildfire. Over extended periods of time (i.e., a disturbance cycle $\approx$ 220 years) the silvicultural systems used in each watershed could be rotated.

Future research

Finally, the results of this study also provide tools to monitor the application of new silvicultural systems in the spruce-subalpine forest types within the SBSdw3, SBSwk1 and ESSFwk2 variants. First, it is unclear whether or not the spatial and temporal patterns of fine-scale disturbance can be mimicked reasonably by silvicultural applications. Long-term silviculture trials are required in these forests types to compare and contrast standard, benchmark indicators of mature, spruce-subalpine forests. Will the application of silvicultural systems intended to mimic natural disturbance at fine spatial scales maintain

healthy forest ecosystems at the stand and landscape levels? Second, an alternative to partial cut silviculture systems was to mimic regionally synchronous disturbance, such as bark beetle infestations, across coarser spatial and longer temporal scales. It would be unrealistic to set up a 200-year long silvicultural trial for monitoring purposes. Long-term forest modelling, however, could provide evidence for the feasibility and ecological appropriateness of such silvicultural systems by comparing predicted states to the current states quantified in this thesis. Third, although the interplay between fine-scale disturbance and intermediate-scale, patch modifying events were important factors of forest dynamics at the stand level, stand replacing fire undoubtedly plays an increasingly important role moving west from the high elevation, wet/cold environments of the subalpine forest to the dry/warm plateau of central British Columbia. At the landscape level, it is expected that the proportion of the land occupied by mature, spruce-subalpine fir forests would decrease and change in spatial distribution on the landscape. What are the historical spatial and temporal distributions of spruce-fir forests on across the central interior of British Columbia? Fourth, it will be important to compare and contrast the silvicultural systems that mimic small- or intermediate-scale events. Snag density and snag class distribution, coarse woody debris (CWD) abundance and CWD size-class distribution, road density and stream crossings, are examples of important variables that should be compared and contrasted at various spatial and temporal scales. Does either system provide a better solution to disturbance based forest management? Is there some other system more appropriate (e.g., clear-cut with permanent reserves)? Is some other form of forest management (e.g., integrated resources management, conservation or zoning) more appropriate? Finally, many conceptual models have been proposed to explain the natural succession of spruce-subalpine fir forest types in western North America. Some explain succession in the absence of disturbance and others maintain

that disturbance is paramount in predicting future stand structure and dynamics. This study has presented further evidence that disturbance is the key driver of change and that steady state communities are actually the minority in many sub-boreal and subalpine ecosystems. Can all spruce-subalpine forest types through western North America really be explained by one succinct successional model? Or, does the stochastic nature of multiple disturbance types working at numerous spatial and temporal scales lead to individualistic succession making it virtually impossible to predict future states?

Conclusions

This research has provided further evidence that fine-scale disturbances are important ecological processes in sub-boreal and subalpine forest ecosystems. Within these ecosystems, however, there is considerable overlap between disturbance types of varying spatial and temporal scales. For example, intermediate-scale disturbance events have played a large role in distinct successional changes in stand structure; more so than that of fine-scale disturbance events. Consideration of disturbance events at multiple scales, however, shows that fine-scale disturbance does contribute to continuous stand level maintenance and renewal; furthermore, that shifts in species dominance tend to be abrupt and due to intermediate-scale disturbances such as those caused by insect outbreaks.

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